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SUBALPINE VEGETATION OF THE WASATCH PLATEAU, UTAH

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INTRODUCTION

Like all mountainous land of the West, the Wasatch Plateau in central Utah is vitally important to people of adjacent valleys. It furnishes their drinking water, the irrigation water on which nearly all their agriculture and industry depends, and summer forage for many of their livestock, as well as timber for local use, opportunities for outdoor recreation, and a habitat for wildlife. As surely as a canyon from the plateau opens upon the valley floor, so surely will one find a farm, a village, or a town. Each of these small islands of civilization is nourished, as by a silver umbilical thread, from snows that accumulate in the nearby highlands. If it were not for the higher-lying, more humid, plateau the arid lowlands would never have been settled, and the flourishing and distinctive communities that the traveler passes through today would not exist.

The subalpine zone of the Wasatch Plateau is of special interest to the ecologist not only because of its bearing on human geography, but because the first studies of the influence of range vegetation on erosion and floods were made here. Forty years ago experiments were begun by the Intermountain Forest and Range Experiment Station which first clearly demonstrated that herbaceous vegetation, and not forest cover alone, had a profound effect on the infiltration and yield of water from torrential storms.

They showed that the abundance and character of apparently insignificant grasses and forbs high on the watershed could mean the difference between the normal streamflow of clear, usable water and abnormal, disastrous mudrock floods (Reynolds 1911, Sampson & Weyl 1918, Forsling 1931). A great deal of additional research in the fields of hydrology, climatology, ecology, agronomy, and forestry, oriented primarily toward rehabilitating depleted vegetation and stabilizing eroding soil, has since been done in the subalpine zone of the Wasatch Plateau.

Despite the fact that much has been learned through this research, the problems of land use of the subalpine zone are by no means solved today. These problems are complex and do not relate entirely to present-day grazing. Much, if not most, of the soil erosion and vegetal depletion that have occurred is due to early-day abuses. Range management during the past 45 years has been only partly effective in arresting this deterioration. The demand for grazing, which becomes progressively greater as the lower zones are depleted of palatable forage, and which is accentuated in places by increasing numbers of deer and elk, conflicts with the need for a stable soil and a perpetually serviceable watershed. In some places the subalpine zone is being drastically overgrazed at the present time. Widespread accelerated soil erosion continues, despite the fact that in many places vegetation has improved materially and erosion has been slowed. The Mount Pleasant flood of July 24, 1946 is an indication of what may be expected in the future unless material changes in management are put into effect. The administrative problem is therefore one of halting deterioration to preserve soil and watershed values, and at the same time satisfying immediate demands for grazing.

The seriousness of the condition of these high range-watershed lands today, after nearly 50 years of administration, is attributable in large part to our ignorance of soil-plant cover relations. In planning and evaluating management it is essential to be able to distinguish between normal erosion and accelerated erosion, but this distinction is in some instances difficult to draw and must be derived from an understanding of soil genesis and plant succession for which basic studies are woefully lacking. It is essential for management to be able to visualize potentialities for vegetal production. At present these potentialities are little understood because the original vegetation has been altered for so long that nobody can remember what it once was like, and the unconscious assumption is made daily in administrative decisions that the present vegetation is normal. The result, as in the selection of mediocre species for judging degree of grazing use, is likely to be continued depletion. Careful ecological research is needed to reconstruct the character of the original vegetation, which can then be used as a key to the potentialities of the land.

The dual administrative need of defining the management objective in terms of plant cover and soil stability poses the problem of the present study. The character of the original subalpine vegetation has never been adequately described. It is the purpose of this paper to present a reconstruction of the original cover of herbaceous uplands, and to outline gross changes that have taken place in vegetation and soil since pioneer days. To be able to do this effectively it is necessary to outline the successional processes involved in development of the original soil and vegetation. This is particularly necessary because of confusion in the literature and in the minds of land managers between primary succession involving soil development on the one hand and secondary succession and accelerated soil erosion on the other.

Accounts of pristine vegetation of the subalpine zone of the Wasatch Plateau are entirely lacking. Father Escalante's route in 1776 lay to the north of the plateau (Auerbach 1943). Warren Angus Ferris (1940) was evidently in Sanpete Valley in 1835, but nothing in his description would indicate that he was on the plateau itself. Frémont (1845) crossed eastward north of the plateau May 29, 1844. Gunnison, following the Old Spanish Trail in part, crossed westward south of the plateau October 13, 1853 (Beckwith 1855). In this account no plant specimens are listed as having been collected west of Green River. There is nothing in the account of the expeditions led by Wheeler and Hoxie in 1872 and 1873 (Wheeler 1889) to indicate what the vegetation was like at the top of the plateau. Search for the original diaries of Wheeler, Hoxie, and their men in the National Archives and Library of Congress has so far failed to reveal anything of value. Dutton (1880) visited the plateau between 1875 and 1877. His account is chiefly of interest to geologists, and his field notes are entirely geological in character.

About all that one can obtain in the way of accounts of early conditions are statements of certain long-time residents. These are obviously not reliable by themselves, but they do corroborate results of studies in the field.

Evidence of the original character of vegetation of the subalpine zone is based primarily upon small areas that have escaped grazing or that have been grazed relatively lightly, and upon changes that have taken place on areas that have been protected during the last three or four decades.

Methods of Study

The field methods used to study vegetation and soil fall into two general categories, depending on the objective: those utilized primarily to give a record of change or trend and those utilized primarily to portray existing conditions, from which in many instances processes of change can be inferred. The former include permanent plots and quadrats, repeat photographs, and range-survey records. The latter include stand descriptions, as well as several methods used to study particular problems. These special methods will be considered later in relation to

their subject matter, but some further consideration will be given now to the methods named above.

PERMANENT PLOTS AND QUADRATS

Of the 52 permanent meter-square quadrats used for studying trends in vegetation, 35 were established, mostly by A. W. Sampson and his associates, between 1913 and 1916. Seventeen were established in 1925 or later. Twenty-one of the 36 major plots (mostly 10 x 10 m) were established between 1913 and 1919, the rest later.

The quadrats and major plots have been examined at irregular intervals since they were established. In some years the quadrats were charted, in other years numbers of plants were listed by square decimeters. By the use of semitransparent overlays in analysis (Ellison 1942a) it has been possible to harmonize these records and obtain a consistent, graphic history of the vegetation. Another device has been to correlate areal extent with numbers of shoots in field work since 1940. These correlations have made it possible to reduce list data (given as numbers of shoots) and of chart data (given in some instances as numbers of shoots, in others as basal area) to comparable terms.

Major plots have been mapped in some years to the extent of showing principal masses of vegetation, but for the most part major-plot data are in the form of estimates of percentage cover and percentage composition. Unfortunately standards of cover estimation have changed greatly during the period of record, so that the major-plot data are useful mostly as a record of changes in proportion, rather than in absolute amount, of the various species.

While the records on these plots and quadrats are not all as uniform or complete as might be desired, they are the most accurate and detailed that are available, and are probably the oldest permanent ecological records of their kind for mountainous terrain in this country. They are in the files of the Intermountain Forest and Range Experiment Station.

PHOTOGRAPHS

Photographs have been made in various parts of the subalpine zone, which date as far back as 1910, but these earliest photographs are few. Most early photographs were taken between 1913 and 1922, many in connection with the establishment of quadrats. These photographs have been very helpful in corroborating evidence of change from permanent plots and quadrats and have been particularly helpful in preserving a record of the character of denuded soil surfaces. During the period 1939-1947 I have rephotographed these same areas. The negatives of these photographs are in the files of the U. S. Forest Service, Washington, D. C.

Aerial photographs of most of the subalpine zone of the Wasatch Plateau have been made. In contrast to terrestrial photographs which have been used primarily to evaluate change, aerial photographs have been used to study patterns in vegetation, soil, and topography. These photographs have revealed the existence of natural and semi-natural areas which, practicably, could have been found in no other way. They have also been of value in giving clues to processes of soil development and plant succession, and in making clear certain geological features of the plateau. Study of the photographs was supplemented by one flight over the plateau in September 1946.

RANGE-SURVEY RECORDS

A range survey of the Manti National Forest was made in the period 1912 to 1914, and a second one in the period 1936 to 1938. By comparing these surveys it is possible to demonstrate certain gross changes in vegetation. The range-survey data consist of estimates of percentage plant cover and species composition for individual vegetal types. As with major plots, estimate methods and concepts of vegetal cover underwent material change in the quarter-century between surveys, and differences in proportion rather than absolute amount are perforce the chief differences that the data reveal.

The range-survey records are necessarily extensive in character, for their purpose was simply to gain an estimate of grazing capacity. Most vegetal types recognized in range survey are larger than 10 acres, and some may cover 1,000 acres or more. In view of the difficulty of making representative write-ups of such large areas and the fact that plant identification is often approximate and sometimes inaccurate, it is clear that only carefully evaluated, major differences can be considered real. By confining comparisons to species that are easily identified, and by accepting only consistent results on many sections of land, a considerable body of fairly sound evidence has been built up. These records have been of particular value in giving a measure of the spread of certain readily recognizable species, such as *Artemisia discolor, Chrysothamnus viscidiflorus*, and *Madia glomerata*. The range-survey records, covering the entire subalpine zone of the Wasatch Plateau, are a valuable supplement to the more accurate, but also much more restricted, permanent plot and quadrat records.

STAND DESCRIPTIONS

The detailed descriptions of communities in this paper are based upon stand descriptions made by the author in 1946 and 1947. These descriptions consist of two parts.

First, an estimate of cover is obtained by sampling the stand with many temporary meter-square plots. On each the proportion of ground covered by living herbage, the proportion not covered by herbage but covered by litter, and the remaining proportion of bare ground are estimated. For each plot the estimates are made rapidly, to the nearest 10%, but enough plots are examined to give what is thought to be a reliable average for the stand. Cover has been deliberately chosen to describe these communities, rather than herbage weight, with full realization of the imperfections of cover estimates and of the fact that weight estimates may be more objective and give a better picture of the forage resource. The chief

reason for this choice is that effective protection against accelerated erosion is more important in the subalpine zone than forage production, and this protection is probably more closely correlated with cover, both of vegetation and litter, than it is with weight.

Estimates of cover are liable to great subjective error because ordinarily they are not based on a rigid standard, as, for example, estimates of weight may be. The point-analyzer, however, does provide an objective standard for areal estimation, and is used to train the estimator's judgment (Ellison 1942b). Meter-square test plots are laid out, and on these proportions of vegetation, litter, and bare ground are estimated, as well as proportions of species making up the cover. The "true" proportions are then determined with the point analyzer. The process is repeated until estimated values fall both above and below standard values, as an indication of freedom from bias, and the range of variation approaches a practicable minimum. Check estimates against point-analyzed plots should be made during the period of field observation, but such checks were not made consistently during this study.

The concept of cover used here is much more strict than that employed by most ecologists because it gives small interspaces between the leafage equal consideration with the leafage itself. This concept follows from the nature of the point-analysis standard upon which estimates are based.

The second part of the stand description consists of an estimate of species composition in terms of areal spread, from visual inspection of the stand as a whole. (Ordinarily percentage estimates of only the most abundant species are made on the small sample plots.) The proportions of the various species are expressed by a scale of cover values. This scale differs from others, e.g., that used by Braun-Blanquet (1932, p. 32) in that it is not based upon coverage of the entire ground surface as 100%, but upon the total amount of vegetation whatever that total may be. The scale is as follows:

R	Rare
x	Less than 1%
1	1 to 5%
2	5 to 10%
3	10 to 25%
4	25 to 50%
5	50 to 100%

As a check on accuracy in applying scale values, estimated percentage compositions of the more abundant species (usually classes 2-5, including average estimates from the small sample plots) are added to the totaled midpoints of the lower classes. The grand total should come close to 100%, and if it is not close, a reexamination of the stand is made.

TAXONOMIC NOMENCLATURE

The names of plants used in this report are based mostly upon identifications made in the Forest Service Division of Dendrology and Range Forage Investigations in Washington, D. C. Many rest upon the determinations of specialists in the National Herbarium and elsewhere. I am indebted, for help with their particular groups, to Arthur Cronquist (*Aster* and *Erigeron*), Carroll Dodge (lichens), Joseph Ewan (*Delphinium*), and Thomas Howell (*Carex*, *Eleocharis*, and *Juncus*).

A systematic list of the vascular plants referred to, with authorities, is given at the end of this report. Although many of these plants have been given varietal status by taxonomists, the convention is adhered to in text and tables by using binomials only. Thus *Chrysothamnus viscidiflorus lanceolatus* Hall & Clements is referred to simply as *Chrysothamnus viscidiflorus*. There are two reasons for this: one to save space, the other to avoid a semblance of precision that seems inappropriate in view of the unsettled status of taxonomic nomenclature in this locality.

Another convention, in grouping plants in the tables, has been to include two biennials—*Descurainia richardsonii* and *Androsace septentrionalis*—with annuals. The reason for this is that these species, which may be annuals at lower elevations, have ecological characteristics that still make them more like annuals than perennials in the subalpine zone. That is, they are most common on disturbed or denuded ground, and they are short-lived and small, supplying but scant cover.

ACKNOWLEDGMENTS

The author's part in the study of the subalpine zone of the Wasatch Plateau began in July 1938 upon assuming charge of what is now the Great Basin Research Center of the Intermountain Forest and Range Experiment Station, and has continued to the present. However, the collection of data utilized in this report, covering as it does nearly 40 years, and requiring, as some of it does, the use of specialized equipment, is necessarily the product of sustained, cooperative effort. Acknowledgment is, therefore, due those predecessors in charge of the Great Basin Research Center—Arthur W. Sampson, Clarence L. Forsling, Raymond Price, and the late Enoch W. Nelson—for supervising the establishment of plots and to 90 or more field assistants, the list of whose names is too long to include here, for the taking of records. I am grateful to Howard W. Lull for measurements of snow-drift direction in the lee of trees in 1946, to A. R. Croft for measurements of wind movement above the snow in 1941, to Olaf C. Olson for counsel in describing soil profiles, to Joseph H. Robertson for his efforts in Washington, D. C. to obtain the diaries of explorers, and to W. A. Dayton for his help in obtaining the published descriptions of type localities for certain species.

THE SUBALPINE ZONE

The Wasatch Plateau is in central Utah between 39° and 40° latitude north and 111° and 111°40′ longitude west. Draining eastward into the Green

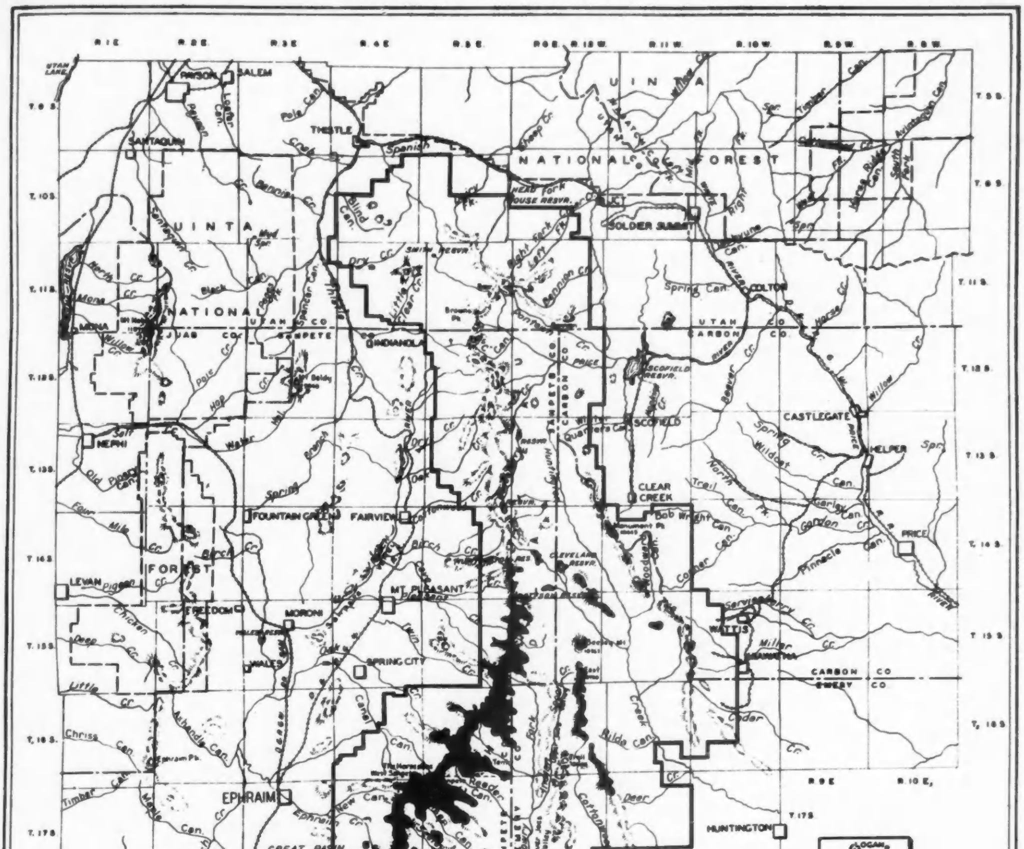

FIG. 1. Map of part of the Manti National Forest embracing the Wasatch Plateau. Solid area is above 10,000 ft. elevation, the higher portion of the subalpine zone. Squares are townships, approximately 6 mi. on a side. Inset shows location of Wasatch Plateau in Utah.

River and then into the Colorado, westward into the Sevier River and Great Basin, the plateau lies between the broad desert valley of Green River on the east and the semiarid Sanpete Valley on the west. It rises from these valleys, which average between 5,500 and 6,000 ft. above sea level at its base to a maximum elevation of 11,282 ft. on South Tent Mountain (Fig. 1).

The subalpine zone is only a small part of the plateau. The zone, as it is considered here, is determined not by rigid altitudinal limits but by characteristic plant communities. It may be thought of as including the land lying above an elevation of 10,000 ft., but extending as low as 9,500 ft. in places, particularly at the northern end of the plateau. The maximum extent of the subalpine zone from north to south is approximately 50 mi. In an east and west direction the subalpine zone may extend along ridges as much as 10 mi. There are some outliers of the main plateau on the east side of the Joes Valley fault that tend to be lower than the main axis; and, judging from the character of their vegetation, they are somewhat drier.

Geology

The Wasatch Plateau is the most northern of the high plateaus of Utah. It lies close to the junction of three physiographic provinces—the Plateau Province to the east and south, the Basin and Range Province to the west, and the Middle Rocky Mountain Province to the north (Fenneman 1931). The top of the plateau is a long, narrow axis lying approximately north and south with a series of riblike ridges extending at right angles from it.

The greater part of the top of the plateau is level or rolling. Most of it is easily accessible to domestic livestock and has been heavily grazed. The eastern ridges are essentially level. The western ridges dip into Sanpete Valley as a result of monoclinal structure. The sides of the ridges are commonly abrupt either as cliffs, talus slopes, or steep slopes of soil and rock from which part of the topsoil has been stripped away in historic times. Slumps and landslides are common.

Concerning the vast geologic erosion that produced the desert lands of the Colorado and Green River drainages and the present aspect of the plateau, Dutton (1880) wrote:

"The eastern front of the plateau is simply a wall left standing by the erosion of the region which it faces. The Tertiary beds upon the summit, as well as the Cretaceous beneath, once spread, unbroken and undisturbed, as far to the eastward as the eye can reach, and thence far beyond the limits of vision. From the strange land which that summit now overlooks at an altitude of 11,500 feet, more than 8,000 feet of Tertiary and Mesozoic strata have been swept away, and the region which has been thus devastated is large enough for a great kingdom. The Wasatch Plateau is a mere remnant of that protracted process, and, so far as it extends, is a mere rim standing along a portion of the western boundary of the Plateau Province.

"The western front of the plateau, then, is a great monoclinal flexure, and its eastern front is a wall of erosion."

Spieker (1946) has described the geologic history of the Wasatch Plateau in detail. The bulk of the plateau is made up of Upper Cretaceous and Tertiary sediments derived from ancient mountains to the west. There were many oscillations of the Cretaceous sea; some of the deposits took place in brackish and fresh water, and some were laid down directly by streams. During part of the Upper Cretaceous, extensive swamps existed that formed thick beds of coal. Flood-plain deposits of gravel, sand, and mud at the end of the Cretaceous, together with lacustrine deposits of limestone, continued into the Tertiary. The Tertiary strata are considered by Spieker to be Paleocene and Eocene. Most of the Eocene, estimated to be 1,500 ft. thick, has been removed from the top of the plateau by geologic erosion, leaving the Paleocene Flagstaff limestone as a capping stratum that is conspicuous in much of the subalpine zone.

The history of the Wasatch Plateau is particularly interesting in that the transition from Cretaceous to Tertiary, in what Spieker calls the North Horn formation, shows no marked break in the geologic record. The lower part of the North Horn contains dinosaurian fossils, the upper part fossils of placental mammals, but the strata are parallel and reveal no evidence of unconformity (and hence orogenic movement) such as that commonly considered a necessary punctuation between major geologic systems.

In headwater basins along the main crest of the plateau there is considerable evidence of glaciation, which has been described by Spieker & Billings (1940). This evidence, in the form of cirques, widened valleys, and moraines, is most striking in the northern half of the plateau. The glaciers were mostly east of the main divide or on north-facing slopes. Spieker and Billings consider this glaciation to have been of Wisconsin age.

The chief source of nourishment for deep, persistent snowbanks today, which lie where the heads of the glaciers were, is snow that drifts eastward and northeastward over the crest of the plateau. In some years certain snowbanks persist all summer long, and it may be imagined that, in a somewhat cooler, moister climate, they could easily grow into counterparts of the Pleistocene glaciers.

Climate

A summary of the climate of the west front of the Wasatch Plateau in its central part has been published by Price & Evans (1937). Less detailed climatic data have been given by Costello & Price (1939), Lull & Ellison (1950), Forsling (1931), and by Sampson (1918). Figures used in the following discussion that are not attributed to these published records are derived from climatic data in the files of the Intermountain Forest and Range Experiment Station.

AIR TEMPERATURE

A wealth of temperature records has been accumulated at the head of Ephraim Canyon since 1913, particularly for summer. Winter temperature data, however, are meager. Published monthly averages for November through April, and the annual average of 32.5°F given by Price & Evans (1937) and by Costello & Price (1939), are therefore weak.

On the basis of rather complete records made from 1935 to 1944 in standard weather shelters, air temperatures at the head of Ephraim Canyon are summarized in Table 1. The pattern of monthly temperatures is fairly symmetrical for the 6-month period, with a crest in July and August. These summary figures suggest a fact confirmed by the daily records, that maximum air temperatures as high as 75°F are seldom attained.[1] The minimum data suggest that freezing temperatures do not ordinarily occur in July and August, but it is clear that in some years air temperature may drop to freezing or below even in these two warmest months. The average length of frost-free period between 1914 and 1934, according to Price & Evans (1937), was 80 days, extending from June 18 to September 6. For the period 1935-44 at the same station, the average length of frost-free period was 84 days, June 19 to September 11.

TABLE 1. Absolute and average maximum and minimum air temperatures (° F) recorded at Alpine climatic station during the growing season, by months, 1935-44 inclusive.

Month	Maximum		Minimum	
	Abs.	Av.	Abs.	Av.
May	64	58.4	6	14.1
June	73	68.6	13	21.9
July	75	73.2	32	36.9
August	77	71.7	26	36.4
September	68	65.6	16	23.5
October	60	55.8	7	12.1

These temperature data are perhaps typical of the subalpine zone of the Wasatch Plateau, but they fail to reflect the great variation that exists from place to place. No comprehensive instrumental study of local variations in temperature has yet been made. By ordinary observation, however, one knows that temperatures vary enormously in different situations, from hot southerly to cool northerly exposures. They may vary even on the same exposure: simultaneous records at two climatic stations in the head of Ephraim Canyon provide an example of this. One, Alpine, is at an elevation of 10,000 ft. and the other, Meadows, 0.4 mi. west of Alpine, is 240 ft. lower. Alpine is on the steeper slope, but both stations have a westerly exposure, and both are on open, untimbered sites. Between May and October in 1943 and in 1944, when the two climatic stations were run concurrently, daily maxima were usually 1° to 3° F lower at the lower station. Differences in daily minima tended to be even more pronounced, minimum temperatures at Meadows averaging about 5° F lower, and sometimes being as much as 11° or 12° F lower, than at Alpine. In contrast to the data given in the last paragraph for Alpine, the average length of frost-free period at Meadows, 1945-49, was only 42 days, July 3 to August 14.

[1] The maximum of 82° F. given by Price & Evans (1937) is an error.

SOIL TEMPERATURE

Soil-temperature records have been kept sporadically, mostly for the summer season. Temperatures of the bare soil surface fluctuate more widely than air temperatures, tending to be higher in the heat of the day and lower at night, but at the soil surface under herbaceous vegetation the amplitude of variation is somewhat less than that of air temperatures (Ellison 1949a, Fig. 11).

Although air temperatures may be very low in winter, soil temperatures are not, because a deep snow blanket protects the soil from freezing. Some spots along the windward side of ridges may be blown clear of snow, and when this happens the soil and rock of these places are undoubtedly affected by frost; but these spots are small. For most of the subalpine zone frost heaving occurs only in fall when the soil is wet and permanent snow cover is not yet formed, and in spring shortly after snow melting. The cold spells at these times are neither intense nor prolonged, and therefore frost heaving does not penetrate deeply, affecting only 2 or 3 cm of the soil of bared surfaces. It has been my experience time and again, when the air is bitter cold in midwinter, that the soil caught in the end of the snow-sampling tube, at depths of from 2 to 6 ft. below the snow surface, is not frozen, although it may contain a few ice crystals. Commonly it is moist and friable.

The fact that the soil does not freeze appreciably in the subalpine zone has a bearing on the application of ecology to range management. Pedestaling of grasses, an indicator of accelerated erosion in the subalpine zone (Ellison, Croft & Bailey 1951), is sometimes attributed to frost heaving. It is true that in the lowlands where snow is shallow, the soil may freeze to a depth of 30 cm or more in an ordinary winter, and there certain bunchgrasses have been observed to be pedestaled as a result of heaving. In the subalpine zone, however, we are dealing with different environmental factors which make frost heaving of firmly rooted grasses unlikely if not impossible.

PRECIPITATION

Average annual precipitation between 1914 and 1934 at the head of Ephraim Canyon is given by Price & Evans (1937) as 28.01 in. From 1935 to 1948 the average was 32.21 in., partly because of relatively high precipitation during the last decade and partly because of improved methods of measurement (Lull & Ellison 1950). It seems safe to conclude that average precipitation over much of the subalpine zone is in excess of 30 in.

Distribution of precipitation by months is markedly cyclic, with a broad crest in late winter (February-April), and a broad trough in late summer (July-September). Precipitation during individual months, however, is highly variable and may depart greatly from this pattern. During the 15 years, 1934-48, June precipitation, for example, varied from 5.08 in. (2.4 times the average for the same period) to zero (Table 2).

TABLE 2. Average precipitation, in inches, at head of Ephraim Canyon.*

Month	1914-34 Av.†	1934-48 Av.	1934-48	
			Greatest	Least
January	3.96	2.88	8.05	1.00
February	2.59	3.99	10.22	1.36
March	4.35	4.06	6.58	2.18
April	3.03	3.83	7.54	1.12
May	1.80	2.26	4.33	0.15
June	0.74	2.13	5.08	0.00
July	1.86	1.60	6.14	0.24
August	1.71	1.72	3.76	0.43
September	1.34	1.38	4.26	0.01
October	1.40	2.46	6.21	0.69
November	2.12	3.27	5.41	0.30
December	3.11	2.61	7.11	0.88
Annual	28.01	32.21		

*Averages for winter months (November through May) in the period 1914-34 are based on incomplete records. Since 1934 consistent year-long records have been kept, or, for certain missing winter months, values have been computed using an observed relation between monthly precipitation totals at Headquarters (8,850 ft. elev.) and Meadows (Lull & Ellison, 1950).:

$$P_M = 1.090\ P_H$$

Until 1941 most records were obtained from Alpine climatic station, 10,100 ft. elev. Since 1941 they have been obtained at Meadows in a more sheltered situation, 0.4 mi. west of Alpine and 240 ft. lower.

†Costello & Price 1939.

To understand the interrelations of climate, soil and vegetation in the subalpine zone it is essential to consider winter and summer phases of precipitation separately.

Winter Precipitation. About two-thirds of the annual precipitation falls, mainly as snow, during the 6-month period, November through April. Average accumulation of snow over the period 1930 through 1947, as measured April 1, varies from 54 to 69 in. on 6 courses (between Sec. 23, T13S, R5E, and Sec. 27, T17S, R4E), and average water content from 18 to 24 in. The averages from the head of Ephraim Canyon for the same period fall about halfway between these extremes, and therefore snowfall here may be considered reasonably representative of the subalpine zone. Table 3 shows the accumulation of snow at the head of Ephraim Canyon up to the first of May. Accumulation commonly continues in excess of melting during April in the subalpine zone, and the bulk of melting takes place in May.

Winter precipitation is the source of year-long streamflow. Practically all the water from melting snow sinks into the ground: only a negligible proportion flows over the soil surface. The effect of this great volume of water on accelerated erosion is therefore slight, except as it bleeds into gullies initially cut by summer storms and keeps them open.

TABLE 3. Average snow depth and water content in inches, on dates indicated, 1940-47 inclusive, Meadows snow course, head of Ephraim Canyon.

	Snow	Water
January 1	33.9	8.4
February 1	47.4	12.5
March 1	60.6	17.9
April 1	68.3	21.8
May 1*	64.6	25.1

*May 1 values are based on a smaller number of measurements than those taken on the regular snow course, although measurements are roughly comparable, being made in the same vicinity.

Summer Precipitation. Summer precipitation contributes little to streamflow, normally sinking into the soil and being utilized by vegetation or evaporated; but in falling on denuded soil surfaces it causes most of the accelerated erosion that is the chief land-management problem of the subalpine zone. Volume of fall is not so important as rate in causing this erosion: sometimes as little as half an inch, falling at high intensity on a sparsely vegetated soil surface, will give rise to overland flow.

Intensities as high as 2.4 in./hr. for 5 minutes have been reported on experimental watersheds near the head of Ephraim Canyon (Forsling 1931). This intensity has been recorded three times in the last 28 years at this station, and on June 25, 1948, storm intensities of 2.40 and 2.76 in./hr. were recorded for two successive 5-minute periods at Meadows, 0.4 mi. to the west. These high-intensity storms are usually strongly localized.

According to Forsling (1931), of 79 storms that were effective in producing erosion on the experimental watersheds at the head of Ephraim Canyon, 36 occurred in July, 26 in August, 15 in September, and 2 in October. Few storms that were large or violent enough to produce severe erosion have occurred in June before a protective vegetal cover has developed. It is fortunate that high-intensity storms are also uncommon during the latter part of the grazing season because, under the severe grazing that has prevailed in the subalpine zone, the soil is essentially denuded in many places after the middle of September.

SOIL MOISTURE

During the period of active snow melting in the subalpine zone the soil is saturated with water. As soon as the snow is melted, gravitational water disappears from the surface soil, and in about 3 weeks it has left the lowermost portion (6-ft. depth) of the watershed mantle (Croft & Marston 1943). Since the soil is charged with all the water it can hold against gravity at the beginning of each growing season, prolonged drought that is cumulative beyond one season is unknown in the subalpine zone.

Measurements of soil moisture at three levels, 0 to 6, 6 to 12, and 12 to 18 in. have been made at the

head of Ephraim Canyon at intervals of a week or 10 days throughout the snow-free period each year between 1924 and 1939. The pattern each year is similar, varying chiefly as occurrence of summer and autumn rainfall varies. The amount of soil water, based on oven-dry weight of soil, declines progressively during the growing season from about 40% in spring to about 15% in autumn. It fluctuates markedly in the surface 6 in. in response to summer rainfall and intervening dry periods. Fluctuation in moisture content at the lower levels is naturally less, although most years of record show the lower levels to be recharged in some degree as a result of summer or autumn storms.

There is a tendency in autumn for soil moisture curves at the 6- to 12- and 12- to 18-in. levels to flatten at about 15%, providing a fairly good estimate of the wilting coefficient. Calculations of the wilting coefficient from moisture-equivalent values (Weaver & Clements 1938, p. 206) give about 17% for surface soil and 15% at the lowest level.

In only one year of record, 1933, did soil moisture drop markedly below the wilting coefficient. In this year precipitation was subnormal throughout the summer. Soil moisture content was reduced to between 13.2 and 16.6%—i.e., to the approximate level of the wilting coefficient—by the end of August, and remained at this level throughout most of September, but then it declined by the middle of October to between 8 and 10%. In some years (6 out of 16) a uniform distribution of rainfall keeps the moisture content of the surface 6 in. above the wilting coefficient all summer long.

WIND

The prevailing wind is westerly, in summer usually from slightly south of west. Measurements of the combs of 15 widely separated snowdrifts near the head of Ephraim Canyon in May 1947 indicate that the late winter wind is prevailingly from N. 80° W., varying from S. 87° W. to N. 65° W.

The air in the subalpine zone is seldom still. According to Sampson (1918), the amount of wind as measured 15 ft. above the ground varied little during the summer months of 1915 and 1916. Sampson's data, given in miles per month, reduce to an average of 8.80 m.p.h. for 1915 and 8.41 m.p.h. for 1916.

Measurements made at the head of Ephraim Canyon between May 5 and June 20, 1941, with anemometers at three heights above the snow, gave the following average velocities in miles per hour:

Height, feet	*Day, m.p.h.*	*Night, m.p.h.*	*24 hours, m.p.h.*
0.5	4.45	3.31	3.88
4.5	7.22	5.92	6.57
12.0	8.24	6.46	7.35

These data show, first, that surficial friction has a pronounced effect in reducing wind movement, and second, that wind movement tends to be greater during the day than the night. Simple observation during the summer months indicates that this latter generality is valid then also.

Between July 23 and August 23, 1941, as part of an instrumental study on Toms Ridge, a Friez 3-cup anemometer was placed so that the centers of the cups revolved in a plane 18 in. above the ground, just clearing the herbaceous vegetation. The site was a typical broad, open ridgetop, with *Stipa lettermani* the dominant species. In the month of record, daily wind movement varied from 1.39 to 5.04 m.p.h. at this level, and averaged 2.76 m.p.h.

Undoubtedly wind movement close to a smooth snow surface is more rapid because of less frictional drag than wind movement close to vegetation. Taking this fact into account, the difference between 3.88 m.p.h. over a snow surface and 2.76 m.p.h. over grassland is explained. Sampson's measurements at 15 ft. above the ground are of the same order as those made 12 ft. above the snow. From the similarity of these measurements, one is led to conclude that seasonal variation in wind velocity in the subalpine zone is probably slight.

Wind is responsible for forming great drifts behind patches of coniferous timber and enormous cornices on the eastern rim of the plateau. These leave their impress upon the vegetation. It is also responsible for deforming trees in exposed places. In the most exposed places a definite krummholz has been formed, and the misshapen trees along the Skyline Drive are a common sight of interest. Although the effects of wind are plainly visible, they are by no means as pronounced as on mountain tops where a definite timberline is achieved and wind velocities are much greater.

EVAPORATION

Measurements made by Sampson (1918) in 1915 and 1916 with various types of atmometers indicated that evaporation in the subalpine zone of the Wasatch Plateau was about the same as in the much warmer oakbrush zone approximately 2,500 ft. lower. The retarding effect of lower temperatures was evidently offset by much greater wind movement in the subalpine zone.

Many measurements of summer evaporation have been made at the head of Ephraim Canyon with Livingston spherical atmometers, and they indicate rapid evaporation most of the time. They are of similar order to the data given by Cox (1933) for mesophytic meadows and fell fields between 10,500 and 13,200 ft. elevation on James Peak, Colorado, although most of Cox's measurements were made in alpine rather than subalpine situations. Measurements made by Daubenmire & Slipp (1943) in subalpine talus slopes and grasslands in northern Idaho are also of similar magnitude. As yet no absolute measurements of evaporation, using vapor-pressure gradients, have been made in the subalpine zone of the Wasatch Plateau.

SOIL

Soil profiles will be taken up in considering the principal plant communities and the problem of concurrent development of soil and vegetation. Here we shall consider some of the surface characteristics

of upland soils with herb dominance on which experimental plots have long been established near the central part of the plateau. For the most part these plots are on level ground or moderate slopes, where soil is naturally fairly deep and rock-free.

Soil parent material is limestone, shale, and sandstone. Limestone and shale are most common in the central and southern parts of the subalpine zone, and accordingly soils are mostly clays and clay loams. Average mechanical composition of 142 surface samples collected from the vicinity of permanent plots in the central part of the plateau is: sand 27, silt 30, and clay 43%. In 1918 J. O. Veatch made a soil map of 3,200 acres in the subalpine zone in the central part of the plateau. The percentages of the total area made up by his soil types, which reflect the general heaviness of these soils, may be summarized as follows:

Clays	23.2
Clays and clay loams	13.6
Clay loams	45.4
Loams and clay loams	9.6
Loams	5.8
Rock ledges	2.4
	100.0

In the northern part of the subalpine zone sandstone is more common and the soils are somewhat sandier.

Gravel content varies greatly, depending largely upon how much accelerated erosion has taken place. About four-fifths of 86 surface samples collected in 1935 and 1936 from near permanent plots contained 2½% or less gravel. If the soils had not been eroded, the proportion of gravel would certainly have been less than this.

Organic-matter content of the surface soil is undoubtedly lower today than it was before accelerated erosion set in. The average of about 100 samples taken in 1935 and 1936, from the surface to a depth of 6 in., was slightly less than 6%. Some of these data are given in Table 4, which shows organic-matter content to vary widely from place to place. Organic-matter content on eroded surfaces was as low as 1.5% in individual samples and in other places exceeded 8%. The average percent total nitrogen was about 0.3, with some samples having as little as 0.1 and others as much as 0.5.

Moisture equivalents for surface samples lie predominantly between 25 and 40%, with an average close to 33%.

Soils in the subalpine zone tend to be slightly acidic. According to determinations made in 1940, pH values range between 5.9 and 7.5, with a modal value of about 6.3. There tends to be a slight increase in pH with depth. This increase probably corresponds to the increase in limestone fragments in the soil which have been incompletely leached, as field tests with acid show. Soil in coniferous timber is in general slightly more acidic than soil of adjacent grasslands.

TABLE 4. Average percentage organic matter in surface soil of herbaceous uplands in the subalpine zone. Figures in parentheses indicate number of separate samples averaged.

Locality (and specific permanent quadrats involved)	SAMPLING DEPTH AND YEAR	
	0-6 in., 1935, 1936	0-1 in., 1940
Bear Creek, Q. 31-34	1.93 (8)	1.74 (8)
Left Fork Enclosure	2.60 (2)	
Becks Creek, Q. 17, 18	....	2.66 (2)
Seely Flat. Q. 27, 28	3.53 (4)	3.69 (4)
Erosion Area A	3.83 (6)	
Philadelphia Flat, Q. 23, 24	3.72 (6)	3.94 (4)
Becks Creek, Q. 19, 20	....	4.01 (2)
Erosion Area B	4.60 (6)	
Little Petes Hole	....	5.00 (4)
Becks Ridge, Q. 13, 14	....	5.49 (4)
Cove Paddocks	5.68 (16)	
Alpine Cattle Pasture	5.82 (20)	
Philadelphia Flat, Q. 25	....	5.87 (2)
Carrying Capacity Pasture, Q. 2-8	....	5.89 (10)
Upper Horseshoe, Q. 21, 22	5.99 (7)	5.25 (4)
Seely Slope, Q. 9, 10	....	6.41 (2)
Wagon Road, Q. M2	....	6.64 (2)
Becks Ridge, Q. 15, 16	....	6.72 (2)
Lower Horseshoe	6.84 (5)	
Meadows	7.33 (4)	

SOIL EROSION

References have been made in this report, and more will be made, to "accelerated" soil erosion. Accelerated soil erosion is conceived to be erosion at a rate greater than normal for the site, brought about by man, usually through reduction of the vegetal cover.

The distinction between accelerated and normal erosion is not always easy to make, but for most of the subalpine zone, where climate permits development of a well-defined soil mantle, the distinction is clear. It rests on the fundamental thesis that formation of a soil mantle is incompatible with the rapid sheet and gully erosion to be seen in most herbaceous communities today. Evidence of accelerated erosion is, basically, evidence of the destruction of a formerly continuous soil mantle (Ellison 1949b).

The following indicators of accelerated erosion are commonly to be observed in the subalpine zone of the Wasatch Plateau (Ellison, Croft & Bailey 1951):

(a) Gullies that have incised the soil mantle.

(b) Pedestaled grasses, and rill marks, attesting rapid sheet erosion from the mantle.

(c) Exposure of "lichen lines" on solidly placed rocks on ridges, attesting abnormally rapid lowering of the general soil level.

(d) Remnants of the soil mantle, like geological outliers, separated from the main body of soil, or from other remnants, by areas of erosion pavement or bared rock.

(e) Alluvial deposits of silt and rock partly burying living shrubs, trees, and herbs that grow upon a normal soil profile. The high organic-

matter content of the surface of the buried profile forms a contrast with the raw, recently deposited material above it.

(f) Aeolian deposits built up in living shrubs, also above a normal profile that sometimes even includes a well-preserved duff layer.

When the statement is made that accelerated erosion has occurred on a certain site, it is based upon observation of one or more of these indicators.

VEGETATION

Herbaceous communities are more extensive in the subalpine zone of the Wasatch Plateau than communities dominated either by trees or by shrubs. Composition of the herbaceous cover varies greatly from place to place. Large areas are dominated by grasses, predominantly *Stipa lettermani. Agropyron trachycaulum, Trisetum spicatum,* and *Hordeum nodosum* are also very common. Other areas are dominated by forbs—*Artemisia discolor, Taraxacum officinale, Achillea lanulosa, Penstemon rydbergii, Geranium richardsonii,* and others. All degrees of combination might be described. Several well-defined communties occur, which may be related readily either to soil moisture supply or grazing pressure, and these will be considered in detail later.

Small patches of Engelmann spruce (*Picea engelmanni*) and alpine fir (*Abies lasiocarpa*) dot the rolling terrain of the higher parts of the subalpine zone and these trees form dense forests on steep northerly exposures. The zone is often spoken of as the "spruce-fir zone," but inasmuch as spruce and fir dominate less area than the herbaceous communities, and because the most critical problems of land use arise in these herbaceous communities, the designation "subalpine" rather than "spruce-fir" is preferable to describe the zone.

Aspen (*Populus tremuloides*), the prevalent species of the montane forest below the subalpine zone, extends into the subalpine zone in small stands, most commonly on south exposures. Limber pine (*Pinus flexilis*) is common on steep, rocky, south exposures.

One of the most common shrubs is *Ribes montigenum,* which forms a fringe around patches of timber. With *R. inebrians* it also forms stands, relatively small in area, on rocky sites. Besides these currants, a mixture of tall shrubs, including *Prunus virginiana* and *Symphoricarpos oreophilus,* often dominates steep south exposures. Like aspen stands on south exposures, these stands of tall shrubs represent an upward extension of communities characteristic of a lower elevational zone. Low shrubs—*Chrysothamnus viscidiflorus, Artemisia rothrockii,* and, particularly toward the northern end of the plateau, *A. tridentata*—dominate some areas of flat or gently sloping ground. Evidence will be given later to show that these low shrub communities are more nearly related to the herbaceous communities of the subalpine zone than to other shrub communities.

RELATIONS BETWEEN TOPOGRAPHY, VEGETATION, AND SOIL

As a concrete illustration of the occurrence of subalpine communities in relation to topography, a transect across part of the head of Manti Canyon may be considered. This transect will also be useful later in providing an insight to normal plant succession and soil development.

The transect is 2 mi. (160 chains) long (Fig. 2). Major plant communities were mapped on a strip extending 5 chains on either side of the transect line.

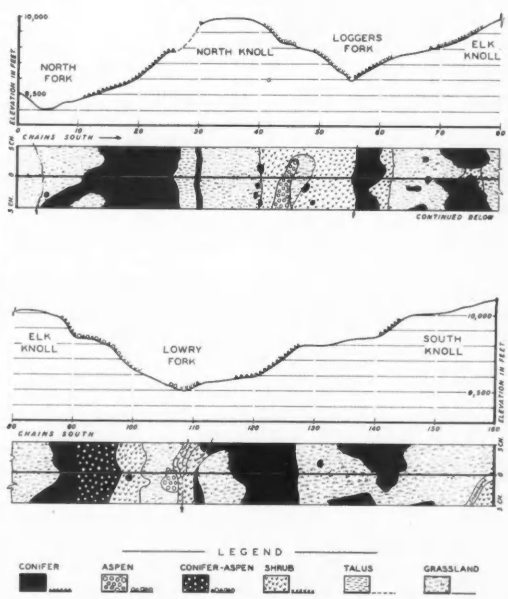

FIG. 2. Topographic profile and belt transect showing major plant communities in relation to exposure, slope steepness, and position on slope. Extent: from ¼ cor. secs. 4, 3, two miles (160 chains) south to ¼ cor. secs. 16, 15, T18S, R4E. Profile lies on center line of belt transect which is 10 chains (660 ft.) wide.

In order to relate the more common communities quantitatively to exposure and degree of slope, they have been classed by 1-chain intervals (or by intervals of less than a chain where these occur, but in no case less than 0.4 chain).

Spruce-fir forests occur usually on north exposures that are rather steep, and alternate with upland-herb communities that occur on more level ground. This alternation is illustrated especially well south of Lowry Fork (110 to 150 ch., Fig. 2) and in Fig. 3. These forested slopes vary from 0 and 5% where soil moisture is probably close to that of a wet meadow at the base of steeper slopes, to as much as 65 and 68%, and average 33% for the transect. In contrast, the slope of herbaceous communities on northerly exposures varies from 1 to 31%, and averages only 14%.

FIG. 3. View southward along transect (Fig. 2) from North Knoll toward Elk Knoll, showing spruce-fir forest and tall-shrub communities on steep northerly exposures alternating with herbaceous communities on gentle slopes. Most of outlying spruce-fir patches on the terrace are either on especially wet or rocky spots. August 10, 1949. F-464265

Spruce and fir are also found on much steeper cliffs and talus on a north exposure (25 to 30 ch., Fig. 2), but here they are scattered, growing where the trees can gain a foothold, not as forests. On south exposures spruce and fir are much less common and occur on rocky, shallow soils of terraces, slopes above terraces, and terrace rims (Fig. 4), often in association with aspen. Aspen occurs mostly on south exposures, often at the base of steep slopes (Fig. 2); *position* on the slope appears to be especially important to aspen in the subalpine zone. On very steep slopes and terrace rims spruce and fir mingle with limber pine. Here the trees are rooted mostly in rock crevices and there is no soil mantle. This is the characteristic site of limber pine.

FIG. 4. View northward along transect (Fig. 2) from Elk Knoll toward North Knoll, showing tall-shrub communities on steep southerly exposures alternating with herbaceous communities on gentle slopes. Note aspens on colluvial material at foot of steep slope in middle distance. August 10, 1949. F-464264

There are three kinds of shrub community on this transect: (1) dominated by *Symphoricarpos oreophilus* and *Ribes inebrians* on south exposures with rocky, colluvial soil (41 to 44 ch., 49 to 55 ch., 98 to 101 ch., Fig 2); (2) dominated by *Sambucus racemosa* and *Ribes montigenum* on north exposures, usually fringing timber on deep soil (60 to 62 ch., 73 to 77 ch.); and (3) dominated by willows in streamside thickets (107 to 110 ch.).

Of these the first is most common in the subalpine zone, and it alternates with herbaceous communities on southerly exposures much as spruce-fir does on northerly exposures. The average slope in this shrub community is 49%, with unit values varying from 39 to 64%. In contrast, the average slope of herbaceous communities on southerly exposures is 12%. On two southerly exposures the transect cuts across areas that are partly herb- and partly shrub-dominated, with an average slope of 30%.

The topographic profile (Fig. 2) is instructive as to the greater importance of topography (and resulting local climate) than of soil parent material in determining plant communities. The strata lie nearly horizontal, limestone and shale alternating in beds of varying thickness and character. An indication of this stratigraphic uniformity is seen in the tendency for a terrace on all slopes at the 9,800-ft. level. Essentially similar soil parent materials, modified by creep and slumping, may thus be expected at the same levels throughout. If one follows a particular level from one end of the transect to the other, say at 9,700 ft., he finds an alternation between spruce-fir on steep north exposures and tall shrubs on steep south exposures. In general, herbaceous communities occur on level areas or moderate slopes irrespective of exposure.

Although these relations of major plant communities to exposure and degree of slope are fairly clear even on casual inspection, the picture is not complete unless one considers at least the gross characteristics of the soils. A striking difference between soils under the different types of cover is the greater rockiness of soils supporting shrubs and trees than of soils supporting only herbs. To provide a quantitative comparison on this point, pits were dug on north and south exposures in each of the canyons, profiles were described, and samples were collected for determination of rock content. These pits were paired at the same elevation on each exposure, one in timber (or in tall shrubs), the other in adjoining herbland.[2] The samples were sifted through a square-mesh Tyler sieve, 4 meshes to the inch, and the percentages by weight of rocks that would not pass were so applied to the horizons from which they were selected that weighted rock content for the entire profile was obtained (Table 5).

This paired-profile design eliminates the variables of exposure, degree of slope, and parent material, since these are the same for each pair. It has a weakness, however, in that the sites selected were on fairly steep slopes, and thus were more typical for shrubland and forest than for herbland which, it will be recalled, is usually found on moderate slopes or level ground. Because these herbland profiles are

[2] The term "herbland" is used in reference to areas having an herbaceous cover in which forbs may be a conspicuous element. It corresponds to "grassland" but without the implication of dominance by grasses or grasslike plants. "Shrubland" would appear to be an equally useful term to denote areas dominated by shrubs.

TABLE 5. Percent of rock by weight in paired soil profiles along transect in Manti Canyon.

Location	Expo-sure	Depth cm	Percent Rock		Expo-sure	Depth cm	Percent Rock	
			Herb	Shrub			Herb	Forest
North Fork....	S.	85	16.2	39.0	N.	100	5.7*	50.7
Loggers Fork...	S.	100	6.6	30.4	N.	70	10.1	11.4
Lowry Fork....	S.	100	3.8	8.4	N.	70	1.3	33.2

*A second herb profile, dug to over 100 cm nearby, had zero rock content.

therefore rockier than usual, the differences in Table 5 are probably less than they would be if more typical herbland soils were being considered.

The shrubland soils are all rockier than the herbland soils, although there is a great deal of variation from place to place in both. The shrubland soils are covered with a distinct layer of duff, 3 to 6 cm deep, in contrast to the rather thin layer of herbland litter. In general zonal differentiation is indistinct, although a break between solum and parent material is fairly clear at 50 cm in the shrubland profile in Fig. 5. In the corresponding herbland profile an indistinct layer of rocks parallels the soil surface at 20 cm, and a gradual structural change from angular block to cloddy occurs. The photographs bring out the marked difference between the two profiles in regard to rockiness.

The forest soils are also rockier than their herbland counterparts, with the exception of the pair in Loggers Fork, where the profiles are unusually alike. A distinctive feature of the forest profiles is the presence of a layer of large rocks at no very great depth, with brown clay or clay loam and an abundance of roots and rootlets in the crevices. Depths to this rocky layer in cm are as follows:

	Herbland	*Forest*
North Fork	55	36
Loggers Fork	45	45
Lowry Fork	55	14

Besides being generally rockier and shallower than the herbland soils (Fig. 6), the forest soils are different in having a duff layer about 6 cm deep, in having a more friable, less compact topsoil, and in being reddish rather than grayish brown.

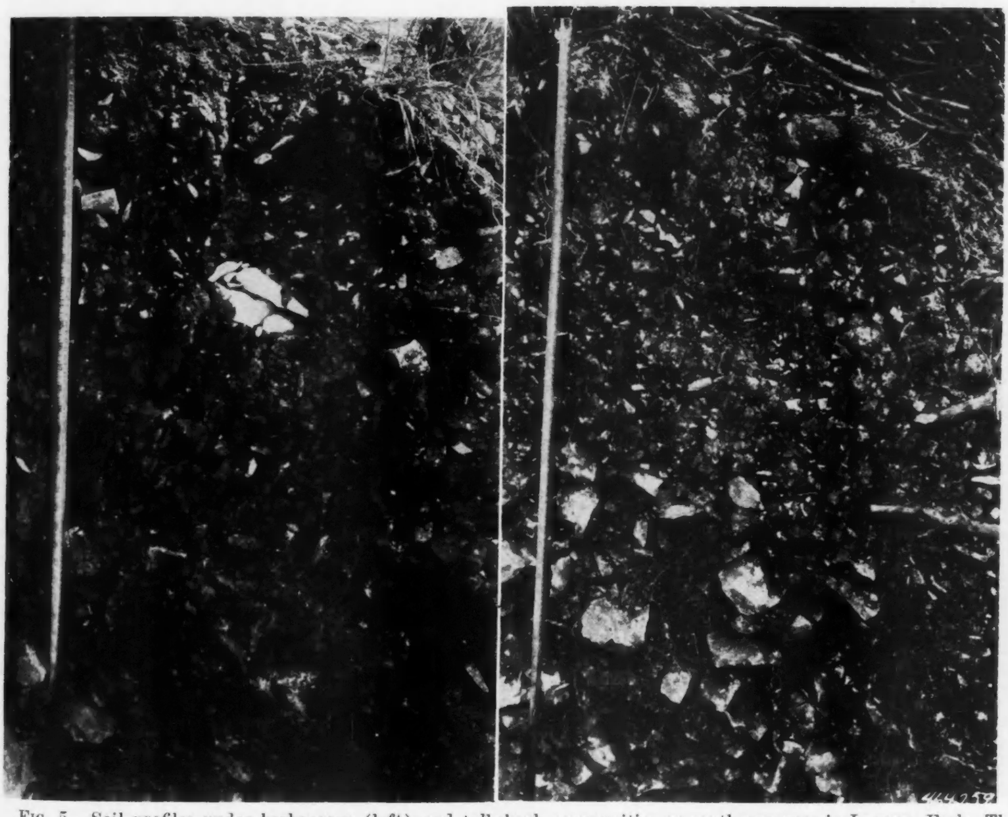

FIG. 5. Soil profiles under herbaceous (left) and tall-shrub communities on south exposure in Loggers Fork. The shrubland profile is much the rockier. A change in structure and rockiness can be seen at 50 cm. A less distinct change occurs in the herbland profile at 20 cm. At 52 ch. on transect (Fig. 2), 9,700 ft. elev.

F-464258, F-464259

FIG. 6. Soil profiles under herbaceous (left) and spruce-fir communities on north exposure in North Fork. Rocks are encountered at 55 cm in the herbland profile, at 36 cm in the forest profile. At about 10 ch. on transect (Fig. 2), 9,500 ft. elev. F-464254, F464253

In short, this transect and the soil pits in the head of Manti Canyon illustrate the general tendencies: (1) for hebaceous communities to occur on gentle slopes with soils fairly free of rocks; (2) for spruce-fir forests to occur on steep northerly exposures with relatively shallow, rocky soils; and (3) for tall-shrub communities to occur on steep southerly exposures with rocky soils. Typical occurrences of areally smaller but well-defined communities—aspens at the base of steep southerly slopes, spruce-fir-limber pine patches on rocky south exposures, and willow thickets along some stream bottoms—are also indicated. This example suggests that in the subalpine zone of the Wasatch Plateau local climate, in combination with subsurface drainage, is more effective than soil parent material in determining the distribution of major plant communities.

This example also contains a suggestion of temporal relations, a bearing on the concurrent development of topography, soil, and vegetation. To grasp this point, it is necessary to restrict ourselves to consideration of individual sites with a given exposure, condition of drainage, and parent material, and to adopt three premises. The first is that development of vegetation, soil, and topography is a concurrent, integrated process in which biotic, edaphic, and topographic factors interact. The second is that, for a given stage in the landform cycle, a gentle slope is ordinarily older and more stable than a steep slope. The third premise is that deep, rock-free soils are older and more stable, from the standpoint of soil development, than shallow or rocky soils. The last two premises support each other: steep slopes tend to have shallower or rockier soils than gentle slopes, their rockiness being a consequence of more frequent slumping. If these premises and restrictions are accepted, it follows that herbland communities, because they are associated with gentler slopes and deeper, more rock-free soils, are more advanced successionally than either shrubland or forest communities. These developmental relations will be considered more fully under "Primary Succession."

PHENOLOGY

Phenological observations, which have been made over many years, have been confined mostly to herbaceous species in the upland-herb association.

Costello & Price (1939), in describing plant development at a variety of elevations in Ephraim Canyon over the period 1925-34, included 7 species in the subalpine zone: *Agropyron trachycaulum, Bromus carinatus, Stipa lettermani, Achillea lanulosa, Geranium richardsonii, Penstemon rydbergii,* and *Viola nuttallii.* Their study, in which the same plants were observed year after year on the same site, emphasizes variation in development from year to year. Stipa, for example, was observed to reach bloom as early as June 24 and as late as August 5, Bromus as early as July 5 and as late as August 10, Agropyron as early as July 18 and as late as August 16. Costello & Price relate these variations to the different dates of snow disappearance which ranged at this site from April 28 to June 15. The average date of snow disappearance was May 5.

A greater number of species was observed in 1942 on 21 sites in and near the head of Ephraim Canyon. Most of these sites were representative of the mixed upland-herb community. Flowering periods by species are shown graphically in Fig. 7.

The species are so arranged in this tabulation as to give a progression in date of beginning bloom. *Caltha leptosepala* which occurred on only one of the 21 sites, should be listed among the early vernal species, for it commonly flowers in icy creek water just as soon as the snow melts. The progression is fairly regular except for a break between early vernal species—Caltha, Claytonia, Erythronium, Thlaspi—and other vernal species at the top of the figure, and another break between autumnal and late autumnal species—Aster, Chrysothamnus, and Bromus—at the bottom. In general, members of the lily and buttercup families bloom early, and composites and grasses bloom late. Castilleja, Achillea, Orthocarpus, and *Erigeron speciosus,* have the longest periods of bloom, while monocots, represented by lilies and grasses, have the shortest.

In 1942 most of the phenological sites were free of snow well before the end of the first week in June and the frost-free period at Meadows climatic station extended from June 28 to September 10. If this period be accepted as a rough average for the 21 sites, it would appear that the first 6 species listed in Fig. 7 had completed flowering essentially by the time the frost-free period began, that the next 7 began flowering before the frost-free period began, and that all species had completed flowering, except for the last 2 listed, when the frost-free period ended.

There is considerable local variation in date of snow disappearance during any one year, depending primarily on topographic factors which influence depth of accumulation and rapidity of melt. Plant development is correspondingly variable from place to place, particularly during the first half of summer. The site on which the observations reported by Costello & Price (1939) were made is free of snow slightly sooner than most because no more than an average cover of snow accumulates there, and because its warm, southerly exposure is conducive to rapid melting. Snowdrifts at the same elevation and within a radius of a mile usually persist for a month or more later. Thus in 1942, snow left this plant development station about June 1, but it did not disappear from a large drift less than a quarter mile away until about July 25. In 1946 the approximate dates of snow disappearance from these same sites were June 4 and July 9, and from another drift still farther away, July 18. The vegetation on sites where these large, late-melting drifts occur tends to be particularly lush. It belongs in tall-forb and wet-meadow communities rather than in the mixed upland-herb community of warm, well-drained sites.

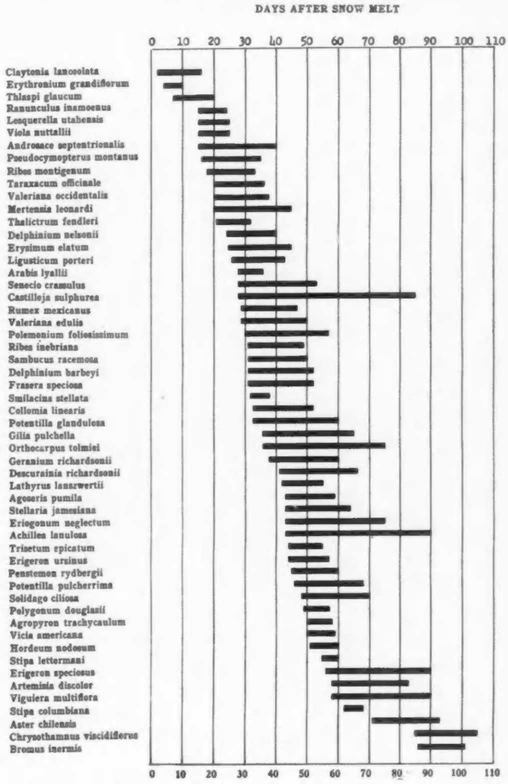

FIG. 7. Average period of flowering of various species near head of Ephraim Canyon, 1942, reckoned from date of snowmelt.

ANIMALS

Unquestionably the most potent biotic factor in the subalpine zone of the Wasatch Plateau today is grazing by domestic livestock—principally sheep and cattle. These animals have been responsible for very marked changes in the vegetation and soil of the subalpine zone as this report will show.

There is no way of knowing exactly what the original grazing animals of the plateau were. It is reasonably certain that mule deer were the principal grazers. Whether elk were originally present is uncertain, but if so they disappeared some time after settlement. The present elk were introduced from the Yellowstone region between 1913 and 1915. In recent years, as a result of restrictions upon hunting, killing of predators, and perhaps other causes, deer and elk have increased greatly. Deer and elk, particularly deer, now exert an appreciable effect on vegetation of the Wasatch Plateau, even in the subalpine zone. Their most obvious influence as yet is observable in the mountain-brush and pinyon-juniper zones where they are forced to concentrate on a narrow winter range between the valley settlements and the deep snow of the mountains.

The larger predators which originally roamed the plateau were the grizzly, black bear, bobcat, cougar, timber wolf, and coyote. The grizzly and timber wolf are no longer present. The others exist on the plateau today, although black bear and cougar are seldom seen. The coyote has survived until recently with numbers apparently unimpaired, in spite of a continual campaign to exterminate him—a campaign which may prove successful, however, with the use of newly developed and more deadly poisons.

The numbers of wild animals on the Manti National Forest, as estimated by forest rangers for 1948, are given in Table 6. The respective hunter kills of deer and elk in 1948, from surveys by the Utah State Fish and Game Commission, were 5,600 and 130.

TABLE 6. Estimated numbers of wild animals on the Manti National Forest, 1948.

Species	Number	Species	Number
Deer	17,000	Porcupine	5,500
Elk	900	Beaver	1,300
Black bear	100	Muskrat	1,100
Cougar	80	Skunk	400
Bobcat	700	Weasel	1,800
Coyote	1,500	Mink	60
Fox	10	Marten	10
Badger	900		

The most common rodents are mice, ground squirrels, marmots, and pocket gophers. Ground squirrels, which occur in colonies, appear to have increased greatly in numbers and distribution in the subalpine zone during the last decade. Marmots are common on rocky ledges and talus slopes. Several different species of mice occur in the subalpine zone. Pocket gophers are common, and because of their conspicuous disturbance of soil they have received some attention. It seems quite clear that the pocket gopher is important as an agent in soil development, in mixing and aerating the soil. He is also a potent factor in speeding accelerated erosion. However, it has been shown (Ellison 1946) that the pocket gopher is not a primary cause of accelerated erosion on the Wasatch Plateau as has been claimed elsewhere. Some information has been accumulated, also, on relations between pocket gophers and native vegetation (Aldous 1945, 1951; Ellison & Aldous 1952).

Many forest birds are to be found in timbered portions of the subalpine zone. In the untimbered portions there are three prairie species of particular interest because they appear to fill the same ecological niches on this high grassland as in the lowlands. Horned larks nest widely in the grassland, sage hens are sometimes encountered, and marsh hawks may be seen on almost any clear summer day soaring over the meadows and uplands just as they do in the lowland valleys.

MAN'S INFLUENCE

It is reasonably certain from the account of Father Escalante (Auerbach 1943) that the Indians set fires promiscuously. That they hunted in the subalpine zone is attested by arrowheads and other artifacts which are occasionally found. It is possible, too, that they harvested certain roots. *Valeriana edulis*, which Frémont (1845) records as a food plant in the valley in 1844, grows in the subalpine zone, and it is possible that this species and others were harvested there by Indians. Although it is therefore evident that Indians roamed the subalpine zone, the extent of the disturbance they may have caused by burning is not known.

The Old Spanish Trail from Santa Fe to Los Angeles, which Auerbach (1941) believes to have been travelled as early as 1807, ran along the east front of the Wasatch Plateau, ascended Ivie Creek to Wasatch Pass, just south of the plateau, and descended Salt Creek to Salina (Beckwith 1855, *map*). Auerbach's map of the Old Spanish Trail shows one branch in Sanpete Valley, but he does not comment upon it. It is possible that horses and mules, which were brought in great numbers from California over the Old Spanish Trail, may have escaped and grazed parts of the plateau prior to settlement. Such grazing, if it occurred in the subalpine zone at all, was probably light and intermittent.

Permanent settlment, bringing heavy grazing pressures by domestic livestock primarily, but also logging, road building, and other influences of the Mormon pioneers, was the precursor of profound and lasting changes in vegetation and soil of the Wasatch Plateau. The first colony in the vicinity of the plateau was Manti, where about 50 families settled November 20, 1849. Population of Sanpete County, on the west side of the plateau, grew at the rate of 345 persons a year until about 1894, when the rate began to lessen; between 1894 and 1920 the rate of increase dropped off. A maximum population, 17,505 persons, was recorded in 1920. By 1950 the population had declined to 13,867.

Recurrent Indian depredations probably kept livestock from grazing in the subalpine zone of the plateau for at least 10 and perhaps 20 or more years after settlement. The last Indian trouble in Sanpete County is said to have ocurred in July 1872 (Whit-

ney 1893). During the first decade after settlement there was probably ample timber in the mouths of the canyons, and ample forage in the valley and foothills, to meet the settlers' needs. By about 1870, with the cessation of Indian troubles and the demands of a rapidly increasing population, intensive grazing of the subalpine zone probably began.

Judging by figures for Utah as a whole, there were very rapid increases both in sheep and cattle until about the turn of the century. According to Reynolds (1911), a gradually increasing business in the grazing of cattle and horses was built up by settlers in the vicinity of the Wasatch Plateau until 1880:

> "The range cattle business was at its height in 1880, when the sheep business first began to take foothold. From the first, sheep were more profitable than cattle for those who were able to secure enough summer range. A long struggle ensued between the sheepmen and the cattlemen, with the final defeat of the latter. Throughout this fight for control of the summer range, tactics were employed by both sides to oust their adversaries, which caused great damage to the range itself. Flocks were handled close bunched in bedding, in feeding, and in maneuvering to obtain control of the choice areas, and were moved over a far greater area than was necessary. Hundreds of fires were set under the mistaken idea of 'improving the range,' and to burn out dense areas of brush in order that the sheep might penetrate them. In the fall, upon leaving the summer range, it was customary to set fires on the way out, and in that way much green timber also was killed.
>
> "As the contest between the sheepmen and the cattlemen, and between rival sheepmen became more severe, the carrying capacity of the range rapidly diminished, and more travel on the part of the grazing stock became necessary to secure enough feed."

The sheepmen were not all local residents. Many of them were transients who would bring their flocks from Colorado (and, with the advent of railroads in Sanpete Valley, from Oregon), follow the snow up the flanks of the plateau in spring, graze northward along the subalpine zone during summer, and ship their sheep from Colton in the fall. Close-herding and excessive trailing, mentioned by Reynolds, were only two of the destructive practices of early graziers. They lambed in the lower mountain zones in spring, and sheared and dipped many of the sheep on the very top of the plateau in summer. Some of the old dipping and shearing corrals may still be seen. The *Ephraim Enterprise* of July 20 and 27, 1892, published two letters "From the Shearers" which tell of their arriving at the head of Cove Creek (elevation 10,000 ft.) July 13, when snow banks were still abundant. The 30 men sheared about 3,000 sheep in two days, and since they expected to be at this camp 12 work-days, it may be estimated that they sheared some 18,000 mature sheep in that one place that year.

Still another element in range deterioration was the unwieldy size of herds. According to James Jensen of Spring City, who herded as a boy around 1880, herds might consist of from 2,000 to 3,000 sheep exclusive of lambs.

The consequence, according to Reynolds (1911) was that:

> ". . . between 1888 and 1905, the Wasatch Range, from Thistle to Salina, was a vast dust bed, grazed, trampled, and burned to the utmost. The timber cover was reduced, the brush thinned, the weeds and grass cropped to the roots, and such sod as existed was broken and worn. The basins at the head of the canyons suffered most, relatively, because they contained the best feed for sheep and were less broken in topography and more easily accessible."

Reynold's calling the plateau "a vast dust bed" is substantiated by old Sanpete residents, who tell of being able to count the herds of sheep on the mountain by the dust clouds they could see from the valley. They corroborate his references to burning, also, and certainly there is abundant evidence in the form of charred stumps, from the oakbrush of the lower slopes, through the montane forest of aspen and fir, to the patches of fir and spruce in the subalpine zone, to indicate that fire was at one time much more common that it is today.

These abuses of the watershed resulted in destructive floods in the wake of torrential summer storms. The first serious flood of this sort occurred in 1889, 39 years after settlement and probably 15 to 20 years after grazing began in the subalpine zone of the Wasatch Plateau.[3]

In the nineties, and perhaps as early as the eighties, complaints arose about the condition of the water supply. In an editorial in the *County Register* for June 9, 1890 headed "The Water We Drink" the unpotability of the town's water is attributed to corrals beside which the open ditches ran, dirty clothes allowed to soak in the ditches, dead animals, and sheep herds in Ephraim Canyon. These conditions, says the editor, are not peculiar to Ephraim but are general throughout the county. In a later editorial (July 17, 1890) he contrasts the former "virgin purity" of the water with the present

> "something, something, but *what?* Not water, for we have been taught that water has neither color, taste nor smell. Has this something color? Look and see; Has it taste? Ugh! Has it smell? Phew!"

Because of the terrific abuse the watershed was receiving, the reserve now known as the Manti National Forest was established in 1903 to control grazing and timber cutting.

[3] According to Reynolds (1911), who obtained his information from a questionnaire sent to old residents in 1910, the first serious flood occurred in 1888. Lever (1898), in a detailed chronology covering the period from November 20, 1849, when the first Mormon families settled Manti, until October 1898 when his book went to press, records no floods until August 16, 1889. This flood is also mentioned by Woolley (1946), and reference is made to it in the Sanpete *County Register* of June 4, 1890 (Vol. 1, No 1.) None of these sources mentions a flood in 1888. Woolley (1946, p. 87) abstracts the Salt Lake City *Deseret News* of September 4, 1852 to the effect that there was a flood in Manti July 30, 1852: "Rain very heavy. Water ran through streets 4 to 10 inches deep. Washed woodpiles, haystacks, etc., before it. Yards and cellars flooded." In view of the fact that this author does not distinguish between torrential storms in town and on the watershed, nor between high stream flow and mud-rock flows, nor between natural floods and those resulting from denudation of the watershed, this "flood" 2½ years after settlement is certainly not to be considered in the same class with those repeated mud-rock flows that began nearly 40 years later

A reliable estimate of the amount of grazing at the time the Manti National Forest was established is probably impossible. Rushton H. Charlton of the General Land Office, who was reported in the *Ephraim Enterprise* of July 23, 1903 to be inspecting the forest, is perhaps the authority for an estimate of 800,000 head of sheep. This same figure, which probably included lambs as well as mature sheep, is given in a petition from local residents to the Secretary of Interior (*Ephraim Enterprise,* September 24, 1903). By later administrative standards, in which lambs are not counted, this figure would represent 520,000 sheep. How many cattle were grazing the plateau at that time is not known even by such a rough estimate.

Livestock were sharply reduced upon establishment of the Forest. In 1905 there were about 150,000 sheep in the Forest. Sheep increased to over 200,000 in 1907 and then gradually decreased to about 100,000 in 1950. The number of cattle in 1905 was 20,000. Cattle increased during World War I to 28,000, and have since declined to a level during the past 15 years of about 15,000.

While there have been many fluctuations in use and a progressive decrease in permitted numbers and in length of season, there appears to have been no radical change in grazing use since the forest was created that is comparable to the first great reduction. Neither has there been any change in management affecting the subalpine zone which is comparable to the change from no regulation prior to 1903 to subsequent regulation. Regulation eliminated transient herds of sheep; reduced the size of herds; established allotments, thereby reducing trailing; protected certain critical areas from grazing altogether; encouraged bedding out (the use of different bedgrounds on different nights, instead of returning again and again to the same spot—a management practice very imperfectly adhered to even at present); provided for better distribution of cattle by salting, developing watering places, and fencing; and retarded very early spring use. These marked early changes in numbers and management suggest why vegetal changes were greater in the first half of the period since 1913, in which year our records of vegetation begin, than they have been in the latter half of this period.

PLANT COMMUNITIES

The plant communities of the subalpine zone will be taken up according to the following scheme:

A. Communities of warm, well-drained sites.
   1. Mixed upland-herb association
      a. Forb-dominated communities on cattle range
      b. Grass-dominated communities on sheep range
      c. Low-shrub communities
      d. Communities of ephemeral species
      e. Erosion-pavement communities.
   2. Limber-pine community
   3. Tall shrub communities
B. Communities of cool and moist or poorly drained sites
   1. Spruce-fir association
   2. Tall forb community
   3. Wet meadow community
   4. Alpine relic community

Original Mixed Upland-Herb Association

Before describing present-day plant communities, nearly all of which have been altered from their original state, it is necessary to portray the character of the pristine vegetation, as well as this may be done from the evidence at hand. The convention will be adopted of including in one major association all the herbaceous communities growing on well-drained sites and soils fairly free of rocks. Certainly the original vegetation was not homogeneous, for many variations in site occur; but changes accompanying disturbance during the past 75 years have been so great, and present evidence of the original vegetation is so fragmentary, that it is not possible to differentiate these original phases.

Another convention will be a restricted use of the terms "xeric," "mesic," and related words. In the usual sense all this upland-herb vegetation is mesic. Hydrophytes are ruled out by the specification "well-drained sites," and there are probably no true xerophytes unless some of the introduced species can be so considered. But there are degrees of mesophytism, and it seems essential to distinguish those sites that have been made abnormally dry by denudation of vegetal cover and accelerated erosion, with their distinctive vegetation, from sites with more normal soil and vegetation. On the abnormally drier sites vegetation is usually sparse and less than 30 cm tall, and the exposed bare ground between plants usually shows evidence of considerable accelerated erosion. This kind of habitat will be termed "xeric." On sites that have not been greatly eroded, vegetation may be anywhere from 30 cm tall to a meter or more, and the cover of living plants and litter so dense that it appears on casual inspection to be essentially complete. This kind of habitat will be termed "mesic." Descriptions of plant communities will indicate the species that characterize these two extremes of habitat.

From the time that the cause of the first floods was recognized the condition of the herbaceous subalpine uplands of the Wasatch Plateau has been a matter of concern. Primarily with relation to this herbland Reynolds (1911) described the effects of grazing in producing floods, Sampson & Weyl (1918) and Forsling (1931) the effects of grazing on erosion, and Sampson (1919) secondary succession in relation to range management. This last study is the only attempt that has been made until now to work out sociological relations of this vegetation, and its conclusions will be considered in detail later in evaluating some of the conclusions of the present study.

VEGETAL COMPOSITION

Six areas that either have never been grazed by domestic livestock or that have been grazed but lightly, at least for many years, provide a partial description of pristine vegetation (Table 7, Fig. 8).

TABLE 7. Vegetal composition of six relic natural areas that have escaped heavy grazing by domestic livestock, at least in recent years.* Abundance symbols are explained on page 92.

Stand No.	982	983	986	928	935	925
Aspect	SE	NE	SW	..	NE	SW
Percent slope	30-50	30-50	30	0	55	5
Grasses and Sedges						
Agropyron trachycaulum	1	1	x	3	x	2
Bromus anomalus	..	x				
B. carinatus	2	1	x	R	3	2
Carex festivella	x	1	x	x		
Melica bulbosa	..	x	..	..	..	x
Poa palustris	x	x				
P. pratensis	x	x				
Stipa columbiana	x	..	x			
S. lettermani	x					
Trisetum spicatum	x	x	..	x	..	1
Perennial forbs						
Achillea lanulosa	1	x	1	1	..	1
Agastache urticifolia	..	..	..	..	3	
Agoseris arizonica	..	x	x			
A. pumila	x	x	..	..	..	x
Angelica pinnata	x	..	..	1	..	1
Aplopappus parryi	..	R				
Aquilegia coerulea	..	R	R	..	..	R
Arabis lyallii	..	..	..	x	..	x
Artemisia discolor	..	..	..	..	1	
Aster foliaceus, A. chilensis	2	..	1	2	..	3
A. engelmanni	..	x	1			
Castilleja leonardi	..	x	x			
C. miniata	..	x				
Cirsium (drummondii?)	1	x				
Delphinium barbeyi	..	2	4	..	1	
Epilobium angustifolium	..	x	..	R		
Erigeron speciosus	x	2	..	4	..	3
E. ursinus	x	..	x			
Erysimum elatum	x	..	x			
Frasera speciosa	..	..	..	..	..	1
Galium boreale	..	x				
Geranium richardsonii	..	R	x	1	x	1
Helenium hoopesii	..	R				
Helianthella uniflora	..	x	R			
Heracleum lanatum	..	2	x	..	1	
Lathyrus lanszwertii	3	3	1	..	..	2
L. utahensis	..	..	..	..	x	
Lupinus alpestris	..	..	..	2		
L. foliosus	1	x				
Mertensia leonardi	4	4	1	1	2	2
Monardella odoratissima	..	..	x			
Osmorhiza obtusa	..	x				
O. occidentalis	..	..	x	x	3	
Polemonium foliosissimum	..	..	R	..	x	x
Potentilla glandulosa	..	..	x			
P. pulcherrima	..	R				
Ranunculus inamoenus	..	x				
Rumex mexicanus	..	..	..	..	..	1
Rudbeckia occidentalis	..	R				
Senecio ambrosioides	x	x	.			
S. (mcdougallii?)	..	..	x			
Silene lyallii	..	R				
Smilacina stellata	1	x	x	1		
Solidago ciliosa	..	..	..	..	..	x
Stellaria jamesiana	..	..	x	..	1	1
Taraxacum officinale	x	x	R	R	R	x
Thalictrum fendleri	1	1	4	1	1	1
Valeriana edulis	x					
V. occidentalis	R	x	x	..	..	1
Vicia americana	1	1	x	..	1	1
Viguiera multiflora	x	x	2	1	x	1
Viola (adunca?)	x	R				
V. nuttallii	..	x	..	..	..	x
Annuals						
Androsace septentrionalis	x	x	x			
Chenopodium album	x	x	x	..	x	x
Collomia linearis	x	x	..	..	R	x
Descurainia richardsonii	x	x	x	..	R	
Epilobium hornemanii	R					
Galium bifolium	..	..	..	..	1	
Polygonum douglasii	..	x	x	..	..	x
Shrubs						
Lonicera involucrata	..	..	..	R		
Ribes montigenum	2	1	3	1	1	1
Rosa fendleri	x					
Sambucus racemosa	1	1	1	..	4	
Symphoricarpos oreophilus	1	1	x	..	2	2

*For cover data see Table 13.
Stand 982. Block Mountain, 10,100 ft. elev., T20S, R4E, S17.
Stand 983. Block Mountain, 10,000 ft. elev., T20S, R4E, S17.
Stand 986. Twelvemile Canyon, 10,000 ft. elev., T19S, R4E, S18.
Stand 928. Twelvemile Canyon, 10,000 ft. elev., T19S, R4E, S18.
Stand 935. Ephraim Canyon, 9,900 ft. elev., T18S, R4E, S28.
Stand 925. Black Mountain, 10,000 ft. elev., T19S, R3E, S13.

One of the most striking things about these natural areas is the abundance of species of perennial forbs and the large proportion they make of the total vegetation. With the exception of stand 935, which has a particularly large proportion of shrubs, perennial forbs make up from 70 to 88% of the vegetation. Grasses and sedges contribute materially to variety, but they make up only between 1 and 21% of the total. Annuals are rather inconspicuous. All these stands contain shrubs, some a fairly high proportion, and we shall return to this point later.

Another outstanding fact, besides the varied mixture of forbs and grasses, is the number of species that are scarce on heavily grazed range except as relics growing in spots protected, or partly protected, from grazing. Such spots are thickets of wild currant, alpine fir, and Engelmann spruce, small coves near the brink of cliffs, and, on cattle range, steep upper slopes. Grasses and a sedge that appear as relics in these protected spots, on overgrazed cattle range particularly, include:

Agropyron trachycaulum	*Carex festivella*
Bromus anomalus	*Melica bulbosa*
B. carinatus	*Poa fendleriana*

Relic broadleaved species in these protected spots, also included in Table 7, are:

Angelica pinnata	*Ligusticum porteri*
Aquilegia coerulea	*Mertensia leonardi*
Castilleja leonardi	*Osmorhiza occidentalis*
C. sulphurea	*Polemonium foliosissimum*
Erigeron speciosus	*Rosa fendleri*
Erysimum elatum	*Solidago ciliosa*
Helianthella uniflora	*Valeriana edulis*
Lathyrus utahensis	*V. occidentalis*

FIG. 8. Stand 983, Block Mountain natural area. Principal species in foreground: *Mertensia leonardi, Erigeron speciosus, Delphinium barbeyi, Heracleum lanatum, Aster engelmanni.* Note association of shrubs and trees with rock outcrops higher on slope. Northeast exposure, 10,000 ft. elev. August 10, 1946.
F-443912

The majority of these are tall and succulent and are relished especially by sheep. *Heracleum lanatum,* listed in Table 7, is only rarely found in the subalpine zone today, even as a relic, probably because the protection given by thickets of shrubs is inadequate for a plant so large and highly palatable.

Another feature of most of these species is that they are characteristic of rather moist sites. Compared with them as a group, vegetation of most of the upland-herb association as it exists under grazing today, is relatively xeric, with the following dominants (in varying proportions, depending on whether sheep or cattle range is being considered): *Stipa lettermani, Taraxacum officinale, Artemisia discolor, Madia glomerata, Penstemon rydbergii,* and *Geranium richardsonii.*

It will be noted that *Madia glomerata* and *Chrysothamnus viscidiflorus* are absent from all these stands, and that *Stipa lettermani, Artemisia discolor* and *Helenium hoopesii,* which are also often abundant on more heavily grazed range, occur in only one of the six. These species, together with *Taraxacum officinale,* will later be shown to have increased in the subalpine zone. Their absence or scarcity in these natural areas supports the inference that they are intruders.

Minor characteristics of vegetal composition probably relate to past grazing of some of these stands. One of the Twelvemile areas (stand 928) probably has never been grazed by domestic livestock. Twelvemile stand 986, the Block Mountain and Black Mountain areas (stands 982, 983, 925) have been grazed, but only occasionally. Ephraim Canyon stand 935 was probably consistently grazed prior to the turn of the century, but appears to have been grazed rarely since. The influence of adjacent heavily grazed range is also detectable. For example, the presence of *Artemisia discolor* in stand 935 is attributable to the washing down of seed from higher-lying range where this species is abundant. Taraxacum is present in minor amount in all six stands, doubtless originating from seed blown in from surrounding range where dandelion is a common dominant. (The very great mobility of dandelion fruit may be gauged by the fact that it has been seen floating in the air near the top of the Wasatch Plateau in March while the ground was still deeply covered with snow. The nearest sources were dandelions blooming and fruiting in the alfalfa fields of Sanpete Valley, distant at least 6 mi. airline, and almost a mile lower in elevation.)

Much of the variation between stands in attributable to the distances that separate them and to differences between sites. Their generally small size is also a factor, and this is reflected by the smallest stands' tending to have fewest species. Stands 925 and 928 are only a few square rods in area, but the others are larger, varying from half an acre to as much as an acre. Small size coupled with proximity to spruce-fir stands is in some instances responsible for the presence of species that have an affinity with conifer timber. *Aster engelmanni, Delphinium barbeyi* (a dominant in the tall-forb community), and *Ribes montigenum,* occur characteristically around edges of timber. *Lupinus alpestris* often occurs abundantly in forest openings also.

It is possible that some of these variations in vegetal composition are related to differences in soil development and successional status. The soil of stand 935 is very rocky, on a steep colluvial slope, and 39% of the vegetation is shrubs. The proportion of shrubs in the other stands varies from 2 to 13%. In contrast, the proportion of shrubs on the more extensive semi-natural area, Elk Knoll (to be described shortly), with a well-developed, fairly rock-free soil mantle, is less than 1%. Abundance of shrubs on these smaller natural areas probably reflects the presence of considerable gravel in the soil (see Fig. 10, a profile in stand 986), rock outcrops within the

stand (Fig. 8), or shrubs associated with rocks or timber bordering the herbaceous stand.

The small proportion of grasses in these stands may also relate to rockiness of the soil, although it it notable that a profile 105 cm deep in the midst of stand 983 with only 10% grasses (Fig. 8) contains very little gravel. Grasses make up about 30% of the vegetation of Elk Knoll.

Representativeness of Relics

These limitations of the small natural areas and occurrence in the shelter of shrubs of the same mesic species that are found on them raises the question, are those relics representative of the upland-herb association as a whole? All the natural areas are surrounded by conifer timber or cliffs, and one might suppose that thickets of shrubs on the grazed range provide a cooler, moister microclimate than prevails in the open. Is the mesic character of these relic species truly the character of the pristine vegetation, or does it reflect a habitat that is unduly favorable?

This is a most important question, and one particularly investigated during this study. The conclusion, that the pristine vegetation *was* more mesic than the vegetation prevailing on the grazed range today, is based upon the following lines of evidence:

1. Certain xeric sites within natural areas are occupied by mesic species.

2. Vegetation of Elk Knoll, protected from heavy grazing for about 50 years, tends to be mesic.

3. Mesic species occur on more recently protected range.

Mesophytes on xeric sites: Parts of stand 982 occupy steep, dry sites. The slope is 50%, exposure southeast. There is no timber close enough to provide shade. Yet a dense growth of *Mertensia leonardi* occupies these sites. Other species include *Bromus carinatus, Angelica pinnata, Lupinus alpestris,* and *Erigeron speciosus.*

Mesophytes on Elk Knoll: Elk Knoll is a flatiron-shaped plateau lying at the head of the North Fork of Manti Canyon, fringed with timber and capped with about 30 acres of grassland (Fig. 3). Three sides are very steep, and the one side that is sufficiently gentle to permit ready access lies so far from water that few cattle traverse it. Elk Knoll was certainly grazed by sheep before they were excluded from Manti Canyon. However, except for grazing by deer and elk and an occasional cow that finds her way to the top of the knoll today, it appears to have been protected since 1903. Elk Knoll is not a natural area, therefore, in the sense of being a remnant of virgin range. The existence of obviously accelerated erosion in places, and of rather extensive stands of *Artemisia discolor,* strongly suggest that at one time it was as heavily overgrazed as the rest of the range. But Elk Knoll has the distinction of being the only large area in the subalpine zone that has been protected from grazing for as much as 50 years. It has the advantage, over other natural areas, of being a fairly extensive ridgetop, comparable as to site with most of the upland-herb community that constitutes the major problem of this study.

Among the dominant species on Elk Knoll (for a complete list see Table 12) are:

Erigeron speciosus	*Carex festivella*
Agropyron trachycaulum	*C. hoodii*
Bromus anomalus	*Helianthella uniflora*
Melica bulbosa	*Ligusticum porteri*
Aster foliaceus	*Mertensia leonardi*
Stipa columbiana	

Other species of particularly mesic character, also uncommon on grazed range, are:

Carex raynoldsii	*Lathyrus utahensis*
Rosa fendleri	*Lupinus alpestris*
Aquilegia coerulea	*Osmorhiza occidentalis*
Castilleja sulphurea	*Polemonium foliosissimum*
Crepis acuminata	*Valeriana occidentalis*

These plants are growing in the open, fully exposed to wind and sun and without possibility of augmented water supply by subterranean drainage. If they can grow in as typical a situation as the top of Elk Knoll, they can also grow on other ridgetops and in the headwater basins of the subalpine zone.

Invasion by mesophytes: At the head of Ephraim Canyon are two pastures under fence. One, the Carrying-Capacity Pasture, of 6½ acres, has been protected from the intensity of grazing received by the open range since about 1926.

Permanent quadrats 2 to 8 were established on this area in 1913. These quadrats were dominated at the time of their establishment, by *Penstemon rydbergii, Poa pratensis,* and *Achillea lanulosa.* Photographs made in 1913 show the vegetation at that time to have been closely grazed and the soil surface exposed and compacted.

Castilleja sulphurea, Solidago ciliosa, and *Potentilla pulcherrima* were first noted on certain quadrats in 1923. By 1930 they had appeared more widely, with *Geranium richardsonii, Agropyron trachycaulum, Stipa lettermani,* and *Arabis lyallii,* among others. Later *Senecio crassulus, Valeriana edulis, Bromus carinatus,* and *Thalictrum fendleri* appeared. Most of these tall species have continued to increase. Their appearance and spread suggest a trend toward the mixed upland-herb vegetation visualized as the original herbaceous cover in the subalpine zone.

The changes to be described in the Alpine Cattle-Pasture (p. 150), the second pasture under fence, give support to this trend and extend it toward the kind of vegetation described for natural areas. Increase under protection of *Valeriana edulis, V. occidentalis, Erigeron speciosus,* and *Castilleja sulphurea* has been noted in the Alpine Cattle-Pasture on permanent plots and quadrats, and the invasion of less mesic habitats by mesic species is also detectable by reference to intensive range surveys and by observation. For example, Mertensia grows most abundantly in the shrubs fringing timber or water-

courses in the Alpine Cattle-Pasture. Plants are also found along down logs extending into the grassland, and occasional smaller and probably younger plants are seen in the adjacent grassland. From such evidence the process of invasion may be inferred readily. Other invading species include:

Lupinus alpestris	*Polemonium foliosissimum*
Erigeron speciosus	*Valeriana occidentalis*
Mertensia leonardi	*Ligusticum porteri*
Osmorhiza occidentalis	*Helianthella uniflora*

The conclusion is drawn from the foregoing lines of evidence, which support one another, that tall-growing, mesic forbs and grasses can grow in subalpine sites now widely occupied by a more xeric upland-herb vegetation. Since they dominate natural areas today and occur throughout the subalpine zone in small spots protected from grazing, it is probable that they dominated the original herbaceous cover.

The restricted occurrence of these mesic species today, together with their presumably more widespread occurrence on the virgin range, has an important implication. This is that one result of overgrazing is a trend toward an increasingly xeric environment. To explain this trend is to state the obvious. Removal of herbage by overgrazing exposes the soil to wind and sun, and consequent loss of the normal litter cover has the same effect. Accelerated soil erosion usually follows, intensifying the induced drought in several ways, from speeding up the loss of cover to causing rainfall that would normally augment the soil moisture supply to be lost as surficial runoff. Under such conditions species that are adapted to a dry environment are favored over those that require more moisture, and a tendency toward xerophytism results.

The microclimate on deteriorated range is probably less like the normal microclimate than that beneath the shrubs which harbor these relic species. It is not the relic plants in the shrubs which should be regarded as abnormalities, therefore, but the common species on the grazed range—*Taraxacum officinale, Artemisia discolor, Stipa lettermani,* and the like. The abundance of most annual weeds and ephemeral species—of *Oenothera flava, Taraxacum officinale,* and other ruderals—and of a grass so xeric as *Stipa lettermani,* is attributable in considerable measure to this altered microclimate. Possibly drier microclimate should rank equally with selective grazing and trampling disturbance of the soil in explaining the changes that have occurred since the white man's livestock began to graze.

Climax Herbaceous Vegetation

Sampson (1919), confining himself almost entirely to upland-herb communities, classified them into four successional "consociations" which he named according to their dominants. He begins his discussion of "The Wheat-Grass Consociation" with two statements about climax vegetation of the subalpine zone:

> "The wheat grasses (Agropyron) broadly considered, constitute the climax herbaceous cover. In the vegetative cover as a whole, however, the wheat grasses are the subclimax type, the timber species, of course, constituting the true climax."

The results of this study necessitate disagreement with both assertions. No evidence was found that wheatgrasses constitute the climax herbaceous cover, and none that the subalpine grassland as a whole will be succeeded by conifer timber as the true climax. Sampson himself presents little evidence that may be interpreted as support for the first assertion (zonation around a bedground, perhaps, *loc. cit.* pp. 58-60), and none for the second.

Sampson is not entirely clear as to the composition of his wheatgrass subclimax. That he conceived wheatgrasses to be essentially exclusive is indicated by a succinct description of "Final or Climax Stage" (p. 4):

> "Deep rooted or densely tufted rather shallow rooted perennial grasses, other vegetation almost entirely lacking."

Speaking of the distance between wheatgrass plants (p. 10), Sampson says:

> "However, regardless of the distance between the bunches, provided the type is fully developed, there is relatively little difference in the character, density, and luxuriance of the other species which inhabit the intervening space, the normal stand of which is usually sparse."

Finally, on page 75, Sampson lists only 4 species as most typical of the primary and secondary species of the subclimax: *Agropyron dasystachyum, A. spicatum, A. tenerum,* and *A. violaceum.* (The latter two names are today included under *A. trachycaulum.*)

On the other hand, the following quotations indicate that Sampson had something besides essentially pure wheatgrass in mind as the climax:

> "The bunch wheat-grass type . . . supports a considerable variety of weeds and other plants, both of deep and of shallow rooted characteristics." (p. 21)

> "In contrast with the turfed wheat-grass type, the conditions that obtain in a normal, fully developed bunch wheat-grass type are such as to permit the presence of other plants of both deep-rooted and shallow-rooted species . . . a few deep-rooted species, like wild bean or alpine lupine (*Lupinus alpestris*), yellow brush, and the like, as well as certain surface-feeding plants, like single-flowered helianthella (*Helianthella uniflora*), mountain squirrel tail (*Hordeum nodosum*), and blue foxglove (*Pentstemon procerus*), occupy the space between the grass bunches where the spacing is fairly wide and the intervening soil not fully occupied by grass roots. Therefore, where the bunch wheat grass stand is opened up by grazing or by other adverse factors, a good balance both of deep and of shallow rooted species, chiefly other than grasses, follows, one set of species predominating at one time and another set at another time." (p. 17)

> "The bunched wheat-grass areas . . . are seldom pure

in stand, and plants other than grasses usually occupy the soil space between the tufts. The nongrasses occur in varying density, depending chiefly upon the available soil water content . . . Precipitation percolates deeply on the rather exposed soils of the bunch-grass areas, and as a consequence both deep-rooted and shallow-rooted species, chiefly other than grasses, are commonly found on bunch wheat-grass areas.'' (p. 67)

Although these statements are contradictory in some degree, this much can be concluded, that Sampson considered the climax herbaceous vegetation to be composed primarily of wheatgrasses.

The concept of pristine vegetation, developed from the observations reported here, which is considered to be climax, differs markedly from Sampson's concept. Instead of dominance by wheatgrasses, with few or no plants of other species, these observations point to a rich mixture of many tall herbaceous species which were widely distributed and among which dominance varied from place to place. Conspicuous species probably included the following:

Agropyron trachycaulum	*Ligusticum porteri*
Angelica pinnata	*Lupinus alpestris*
Aplopappus parryi	*Melica bulbosa*
Aquilegia coerulea	*Mertensia leonardi*
Aster foliaceus	*Osmorhiza occidentalis*
Bromus anomalus	*Poa fendleriana*
B. carinatus	*P. reflexa*
Carex festivella	*Polemonium foliosissimum*
C. hoodii	*Potentilla glandulosa*
C. raynoldsii	*P. pulcherrima*
Castilleja leonardi	*Ranunculus inamoenus*
C. sulphurea	*Senecio cymbalaroides*
Delphinium barbeyi	*Solidago ciliosa*
Erigeron speciosus	*Stipa columbiana*
Geranium richardsonii	*Thalictrum fendleri*
Helianthella uniflora	*Valeriana edulis*
Heracleum lanatum	*V. occidentalis*
Lathyrus lanszwertii	*Vicia americana*
L. utahensis	*Viguiera multiflora*

Species that were probably scarce or absent in the original vegetation, but that have become abundant following overgrazing include:

Androsace septentrionalis	*Lepidium densiflorum*
Artemisia discolor	*Lesquerella utahensis*
A. rothrockii	*Madia glomerata*
Chenopodium album	*Oenothera flava*
Chrysothamnus viscidiflorus	*Polygonum douglasii*
Collomia linearis	*Pseudocymopterus montanus*
Erigeron ursinus	*Rudbeckia occidentalis*
Geranium richardsonii (on cattle range)	*Stipa lettermani*
Gilia pulchella	*Taraxacum officinale*
Helenium hoopesii	*Thlaspi glaucum*

The evidence for the increase of many of these species will be given later in this report. Most of them are particularly abundant on eroded sites or in stands of subnormal cover. The annuals, except perhaps Madia, were generally more abundant 30 to 40 years ago than today. Androsace and Oenothera have probably been decreasing in abundance also, judging from quadrat records, major plots, and range-survey comparisons.

COVER

The cover provided by the original vegetation can be estimated from three lines of evidence: (1) cover on natural areas; (2) cover where evidence of accelerated erosion is lacking, and (3) infiltrometer studies.

Reasoning from the existence of a well-developed soil mantle on upland herb sites throughout the subalpine zone, it must be concluded that the pristine vegetal cover practically everywhere was dense enough to prevent soil erosion of the order that occurs today. Development of a soil mantle is incompatible with a rate of erosion that produces rill marks, gullies, and pedestaled plants year in and year out, over extensive areas. Such visible, widespread erosion causes topsoil to be lost at a much greater rate than the profile can deepen in place by genetic processes.

Table 8 presents average cover in the six natural areas of Table 7. Total cover of vegetation and litter varies from 89% on the Ephraim Canyon area to about 50% on the Twelvemile areas. On the Twelvemile areas pocket-gopher activity is especially pronounced, and the ground, which is very loose and soft, is partly protected by gravel on the surface None of the usual signs of accelerated erosion have been detected on any of these areas.

TABLE 8. Average percent cover of vegetation and litter, as compared with bare ground, on upland-herb natural areas. For plant composition and location see Table 7.

	Block Mountain		Twelve-mile		Ephraim Canyon	Black Mountain
	982	983	986	928	935	925
Vegetation	57	56	36	30	78	60
Litter	17	14	13	20	11	10
Bare ground and rock	26	30	51	50	11	30

Estimates of cover on the upland-herb vegetation of Elk Knoll as a whole and on four included, homogeneous stands where the soil showed little or no evidence of accelerated erosion, were made in 1946. The data are summarized in Table 9. Total cover of all stands was well over 50%. The fact has already been mentioned that parts of Elk Knoll still show evidence of accelerated erosion. This accounts for the lower average cover for the entire knoll than for individual stands. Of the individual stands, slight evidence of accelerated erosion was noted on 973, and on a small part of 969. No such evidence could be detected on 970 and 971.

To appreciate how far these values differ from the cover of comparable overgrazed range, Table 10 should be compared with Tables 8 and 9. Block Mountain stand 984, on overgrazed sheep range but a somewhat better site than the Block Mountain natural areas (Table 8), has only about two-thirds their cover. Ridge, a site originally comparable to Elk

TABLE 9. Average percent cover of vegetation and litter, as compared with bare ground, upland-herb communities on Elk Knoll, 1946.

	Entire Knoll	Individual Stands			
		973	969	971	970
Vegetation	34	37	43	42	40
Litter	24	26	26	26	31
Bare ground and rock	42	37	31	32	29

TABLE 10. Average percent cover of vegetation and litter, as compared with bare ground, upland-herb communities on grazed range, 1946.

	Block Mountain	Ridge			Swedish Knoll	
	984	977	978	976	980	979
Vegetation	37	19	25	24	19	23
Litter	12	11	9	26	11	22
Bare ground and rock	51	70	66	50	70	55

Knoll, is grazed by cattle. The three stands on Ridge, 977, 978, and 976, are progressively farther from water, and accordingly each is grazed less heavily than the one before it: they show a progressive increase in amount of total cover. The data from comparable sheep range nearby, on Swedish Knoll, are similar. The greatest amount of cover of these five grazed stands is markedly less than that of any individual stand on Elk Knoll, even the sparsest; and most of them clearly show evidence of sheet erosion.

For several years the Division of Watershed Management Research of the Intermountain Forest and Range Experiment Station has utilized artificial rainfall in studying the effects of herbaceous plant cover on runoff and erosion. The results of some of this work have been reported by Woodward (1943). Various modifications of the Department of Agriculture F-type portable infiltrometer have been used, and size of plot, method of estimating cover, and application of the "rain" have varied somewhat in the course of the tests. Despite these variations the results are essentially consistent.

In all the tests, surface runoff plotted against amount of cover gives a hollow curve—much runoff being associated with sparse cover and little runoff with dense cover. Soil losses follow the same pattern. It is notable that a point is reached, usually between 50 and 75% cover (combined vegetation and litter) where runoff and erosion are very small and practically constant. An example follows (Bailey 1947):

Total cover, leafage and litter, percent	*Runoff, percent*	*Erosion, tons/A/hr*
9-10	73	5.50
30-35	14	0.50
60-75	2	0.05

The increase in cover from the first class to the second is accompanied by a marked reduction in runoff and erosion; the increase in cover from the second class to the third by a smaller reduction. At the third point both curves have become essentially flat. Since the magnitude and intensity of storms used in the infiltration tests were patterned after those of high-intensity natural storms in this area, the results suggest the minimal cover needed to permit the later stages of normal soil development.

The infiltrometer results confirm the observation that evidence of accelerated runoff is seldom found after natural storms in stands having more than 50% cover. It may be concluded that pristine subalpine cover in the upland-herb association, living vegetation and litter combined, was well in excess of 50%, and probably on the order of 75%.

Vegetal Dispersion. The dispersion of vegetal cover—and conversely, of bare spaces—is notably uniform in all upland-herb natural areas that have been found. The bare spaces, although they may aggregate as much as 30% of the surface under excellent cover, are individually small and are so intermingled with herbage and litter that it is obvious they can have no great permanence.

In contrast, the cover of heavily overgrazed range is often very patchy, dense masses of vegetation alternating with large, persistent areas of essentially bare ground. The masses may be dominated by shrubs or by rhizomatous species—commonly *Penstemon rydbergii, Achillea lanulosa, Artemisia discolor,* or *Erigeron ursinus.* The interspaces may not be absolutely bare, but because of the sparse stand of ephemeral species they support they become essentially bare in late summer when likelihood of erosion is great. As a result, both of erosion from bared spaces and of deposition in perennial patches, differences in soil level are produced that testify eloquently to permanence of the bare spaces. The cover of the perennial patches may be more than adequate to protect the soil immediately beneath, and when averaged with the ephemeral vegetation may give a misleadingly high average cover for the stand as a whole, but nevertheless the cover is not adequate because its dispersion is poor. Stand 984 (Table 10) is an example in which the presence of dense Sambucus patches lowers the actual proportion of bare ground from 57.5% in the interspaces to an over-all average of 51%.

Repeat photographs and records from permanent quadrats show that with lessening of grazing perenials tend to invade the interspaces. As a result dispersion of vegetal cover becomes increasingly uniform, and eventually all trace of the former patchiness may be lost. On certain sites this invasional process is exceedingly slow, even with complete protection from grazing. This is attributable mostly to adverse microclimate at the surface of the bared soil (Ellison 1949a).

From the observedly uniform dispersion of cover in natural areas, from the abnormal erosion of bared spaces on deteriorated range with patchy vegetation, and from trends toward more uniform distribution during range recovery, it may be concluded that pristine cover was highly dispersed.

Crownspread. The height and erectness of pristine herbaceous vegetation, as exemplified today in natural areas, appear to have particular significance to soil and watershed protection. During rainstorms and windy weather generally, when the plants are blown slantwise or almost flat to the ground, it seems probable that the area they cover is materially increased, and that foliage cover is applied more effectively than in calmer weather over such openings as may exist between plants.

Estimates of cover by the method used in this study do not adequately evaluate this aspect of cover-effectiveness. A cover of tall vegetation like that of stand 986 (Table 8) is probably more effective in protecting the soil than an equivalent cover of lower vegetation like that of stand 984 (Table 10), aside from the fact that the latter vegetation is less well dispersed. Other methods that have been used, however, are even more misleading. This is particularly true of measurements of basal area or of number of shoots per unit area. Quadrat charts, from formerly heavily grazed range that has been put under protection, may show a decrease in basal area or numbers of shoots when, actually, effective cover from crownspread has increased because of an increase in taller but sparser vegetation. The decline of *Poa pratensis* and *Penstemon rydbergii,* together with the invasion of taller, more mesic species, on the Carrying Capacity quadrats is an example.

Litter. Accumulated litter in this upland-herb vegetation is not particularly deep. Evidently litter decays rapidly, because little that is more than one year old can be seen on the ground.

It is hard to say just how much litter accumulated in the pristine herbland, or how much is necessary for soil protection, because the figures given in the preceding tables have an inherent bias. Total litter cover is not estimated, but only that part not already screened by living vegetation. Thus Block Mountain stand 983 has only 14% litter (Table 8) but obviously a foliage canopy of 56% hides a great deal of litter besides.

Grasses are decidedly more productive of litter than forbs. For example, consider the two stands on Swedish Knoll:

% of total surface	*979*	*980*
Vegetation	23	19
Litter	22	11
Bare ground	55	70
% of vegetation		
Grasses	65	23
Forbs	35	77

Cover of living vegetation is not greatly different between these two stands, but composition is materially different. About two-thirds of stand 979 is made up of grasses and three-fourths of 980 is forbs. With this difference the litter cover is correlated: the stand with more grass has twice the litter cover of the other.

A more comprehensive example is given by the temporary meter-square plots used to estimate ground cover on Elk Knoll in 1946. On each plot vegetation, litter, and bare ground were estimated to the nearest 10% and totalled to 100, and the proportion that grasses made of the total vegetation was also estimated. The estimates of litter and of grasses are thus completely independent. The correlation is positive and essentially linear ($r = .51$, $P = .000005$). The regression equation

$$Y = 0.34x + 1.00$$

shows that for each 10% increase in proportion of grass (x) in the cover, litter cover (Y) increases 3.4%.

As another example, thirty 6- x 6-foot infiltrometer plots at the head of Ephraim Canyon were point-analyzed for cover in 1949. The proportion of grass in the vegetation varied from 3.0 to 98.9%, and the amount of litter, not counting that under foliage, from 6 to 46% of the ground cover. When the two variables are correlated, a coefficient of $r = .59$ ($P = .0005$) and a regression equation of

$$Y = 0.22x + 12.57$$

are obtained. In this case, for each 10% increase in proportion of grass, litter cover increases 2.2%.

Evidently the foliage of grasses is more resistant to decay than that of forbs. A plausible explanation is their higher content of fiber. For summer-range plants in northern Utah, Stoddart & Greaves (1942) report that the fiber content of grasses averaged 36% in September, compared with 24% in forbs. Most of the species found in the two foregoing examples are not included in these analyses, but several are, and there are others sufficiently similar so that application of this broad conclusion seems valid.

In managing this upland-herb vegetation for maximum watershed protection one might well conclude that a high proportion of grasses in the stand should be encouraged, because of the litter they produce.

SOIL

Although there is variation in the soil profile from place to place in the upland-herb association, there are certain characteristics common to almost all profiles of shale or limestone origin, so long as the soil is still reasonably intact. These characteristics also apply to soils with sandstone parent material, providing considerable clay is included. There is a dark, sandy soil, however, evidently associated with a gypsaceous parent material and a sandy substratum that is notably light and porous; this is deep and loose, and shows less marked differentiation in structure and color than the more common, heavier soils. It supports a notably sparser vegetation too.

Figure 9 shows the characteristics of four soil profiles from the upland-herb association.

Profile 969, on a slight northerly exposure, shows a fairly clear differentiation between solum and weathered parent material (at 40 cm), as most of these soils do, primarily in point of greater rockiness and lighter color. Organic matter decreases, and soil structure becomes coarser, progressively from the surface downward. In this profile there is a distinct tendency for clay to increase with depth which, together with the scarcity or rock in the solum, is taken as evidence of relative maturity. At the top of the C horizon there are more rocks than in the solum immediately above or in the parent material immediately below. In this particular profile the rocks are fragmented, but in many other profiles they are large, on the order of 20 cm in diameter, and they tend to lie flatwise, in a distinct band parallel with the surface.

In profile 986 (Fig. 10), from a westerly slope of 30% about 100 yards below a limestone cliff, the solum contains many small rocks, and to this fact are related the presence of appreciable amounts of lime and a basic reaction throughout. Because of the skeletal material this soil might be supposed to be immature, but there are other considerations. One is the depth of solum, which is about the same as in soils with less skeletal material. Another is the sharp break in rockiness, color, and organic-matter content at 65 cm. A third is the increase in clay content with depth. In light of these indications of maturity it appears unlikely that the gravel in the solum represents original parent material. More probably this gravel has been derived from rocks falling off the cliff at the head of the slope, and the rock fragments have been mixed with the soil by pocket gophers.

An important similarity between this and other upland-herb profiles is the presence of rather large rocks lying just above the parent material in the 45-65 cm zone. Darker soil from above penetrates the crevices between these rocks as it does in many other profiles examined.

Both of these profiles have developed on colluvial materials. Profile 971, however, has developed in

PROFILE 969
Elk Knoll, 10,100 ft. elev., T18S, R4E, S10.

Description	Sand	Silt	Clay	OM	pH	EC	EH	$CaCO_3$
Soil surface, 0 cm.								
Dark grayish brown silty clay loam to silty clay; granular; rather compact; abundant roots; practically no rocks.	19	43	38	7.8	5.6	36.2	4.0	0
	14	43	43	5.6	5.7	35.6	3.9	0
−20 cm.								
Yellowish brown clay; angular nut, faces of blocks stained with organic matter; compact; many roots; very few rocks.	11	34	55	2.4	6.3	42.2	1.4	0
−40 cm.								
Grayish brown mottled with yellow, silty clay to clay; angular block; tight; few roots; many fragments of limestone and chert.	15	42	43	2.0	7.3	33.4	...	16
	16	42	42	1.1	7.4	27.4	...	25

PROFILE 986
Twelvemile Canyon, 10,200 ft. elev., T19S, R4E, S17.

Description	Sand	Silt	Clay	OM	pH	EC	EH	$CaCO_3$
Soil surface, 0 cm.								
Dark grayish brown, clay loam; granular-nut, slight tendency toward prismatic; friable; many roots; many limestone fragments, mostly less than 3 cm. in diameter.	21	50	29	7.9	7.3	43.1	...	4
	16	46	38	6.2	7.2	43.4	...	4
−45 cm.								
Grayish brown clay loam flecked with white and tan; no evident structure; compact; few roots, many rocks, mostly more than 6 cm.	21	47	32	4.7	7.4	35.9	...	18
−65 cm.								
Ashy tan limestone in fragments of all sizes; interstices filled with clay; no structure; a few large roots.	33	41	26	1.4	7.8	10.1	...	54

PROFILE 971
Elk Knoll, 10,200 ft. elev., T18S, R4E, S10.

Description	Sand	Silt	Clay	OM	pH	EC	EH	$CaCO_3$
Soil surface, 0 cm.								
Brown clay; granular; friable to compact; many fine roots, decreasing downwards; no rocks.	19	39	42	8.0	6.3	41.6	2.2	0
	19	39	42	6.4	6.8	42.1	0.5	0
−40 cm.								
Brown clay with slight yellow mottling; prismatic; tight; a few roots; few rocks. −50 cm.	17	39	44	4.0	6.9	42.2	0.4	0
Yellow silty clay mottled with gray and brown in crevices between large horizontal blocks of limestone; inclusions of soft limestone white to yellow; no structure, tight; few roots.	16	42	42	3.6	7.2	40.7	...	6
	19	50	31	2.1	7.5	27.5	...	24

PROFILE 985
Potters Canyon, 10,000 ft. elev., T15S, R5E, S25.

Description	Sand	Silt	Clay	OM	pH	EC	EH	$CaCO_3$
Soil surface, 0 cm.								
Light brown loam; granular; compact because of trampling by sheep; many fine roots; no rocks.	44	35	21	3.2	6.1	13.1	2.6	0
−25 cm.								
Medium brown loam; granular-nut; compact, roots fairly abundant; few rocks.	46	31	23	1.5	6.0	11.5	1.1	0
−60 cm.								
Dark brownish gray silty clay loam mottled with orange, yellow, and black; no structure; tight; few roots; besides sandstone, small rocks of hard blue limestone and some shale.	19	42	39	1.2	7.3	19.5	...	17

FIG. 9. Four soil profiles from upland-herb communities in the subalpine zone. Analytical data are derived from samples, usually 10 cm. deep, in positions shown in profile. Mechanical analysis percentages are exclusive of rock over 2 mm diam.; organic matter (OM) and lime content ($CaCO_3$) are in percent; and exchange capacity (EC) and exchangeable hydrogen (EH) are in millequivalents per 100 gm of dry soil. Horizontal solid lines indicate soil surface and division between solum and parent material; broken lines indicate minor zonal divisions.

place on a level ridge (see Fig. 16). The solum is almost completely free of rock and shows characteristic changes in structure, consistency, color, and organic-matter content from the surface downward. The large blocks of limestone at the top of the C horizon (50 cm), which lie upon rock-free clays extending to a depth of at least 150 cm, are a prominent feature of this profile, and may correspond to the layer of rocks noted in other relatively mature soils.

These three profiles are reasonably intact, although it is probable that some of the topsoil of profile 969 may have been eroded years ago when Elk Knoll was grazed. Their high content of organic matter in the 0-10 cm levels is in marked contrast to most of the organic-matter data in Table 4 from soils on grazed range, and this difference indicates something of the extent to which heavy grazing and accelerated erosion have changed the characteristics of surface soil in much of the subalpine zone.

The texture of profile 985 is markedly lighter than of the foregoing three because sandstone is abundant in the locality (north-central part of the plateau) as a parent material. This soil, in the flat bottom of a glaciated headwater basin, is thought to be colluvial in origin. It changes but little in color, consistency, or structure, until the parent material is reached, at 60 cm. Its organic-matter content is remarkably low, probably because of long-continued denudation of the vegetal cover by overgrazing. However, because of the topographic situation and the texture of this soil, I doubt whether it has been greatly affected by either accelerated erosion or accelerated deposition.

FIG. 10. Soil profile 986, natural area at head of Twelvemile Canyon. Dark soil mantle 0-45 cm, rocky transition to parent material 45-65 cm, parent material 65-100+ cm, 10,000 ft. elev. See Fig. 9. F-443924

Still a fifth profile, No. 962, also on level ground, is described in Fig. 28. Although the vegetation here is dominated by *Artemisia rothrockii,* this shrub, for reasons that will be given later, is considered to be an invader following overgrazing. Certainly the soil is very similar to other soils of the upland-herb association. Residual in origin, it shows characteristic lightening color, lessening organic-matter content, coarsening structure, and increasing compactness, from the surface downward. A zone of large rocks is encountered at 45-58 cm, and this has been included in the bottom of the solum because of the dark soil that extends between and below these rocks. This is the characteristic rocky zone of transition noted in profiles 969, 986, and 971.

In the solum of only one of these profiles—No. 986, which contains limestone gravel throughout—is a basic reaction indicated. In all the others pH is slightly on the acidic side.

The sandy profile, No. 985, shows the smallest exchange capacity, doubtless because it has the smallest proportion of colloids. The exchange capacity of the solum in the other profiles is high, 35 millequivalents or more. The sudden drop in exchange capacity at the C horizon in profiles No. 986 and 962 is perhaps correlated with the sudden drop in organic-matter content. In profiles No. 969 and 971 both exchange capacity and organic-matter content decline more gradually with depth. The increase in exchange capacity at the bottom of the solum in No. 969 and in the C horizon of No. 985 is doubtless a reflection of the increase in clay. Considering the small amounts of exchangeable hydrogen indicated, it is clear that the colloids in all these soils—even in No. 985—are nearly completely saturated with bases.

From these examples, and examination of many other soil profiles in the subalpine zone, there is little evidence of a well-marked B horizon. The only convincing evidence is the tendency for clay to accumulate at depth, and, as the examples show, this tendency is not marked. If a zone of illuviation were present, representing a radically different process from the zone of eluviation lying above, one would think it should be distinguishable. Considering how much water filters down through these soils every spring to aquifers, and thence into springs and streams, however, it is conceivable that material leached from the topsoil may be carried away in solution and not precipitated in a zone of illuviation at all.

The leaching action of snowmelt must certainly be considered one of the dominant soil-forming factors in the subalpine zone. However a high degree of base saturation indicates that the soils are not impoverished by this leaching. Perhaps this soil fertility is a reflection of the influence of herbaceous vegetation in restoring bases to the surface.

The activity of pocket gophers in mixing the soil may be partly responsible for the lack of zonal development within the solum. It has been estimated that pocket gophers bring to the surface some 6 tons of soil per acre annually (Ellison 1946). Soil mixing, probably of a similar order, takes place below ground in the plugging of tunnels. Weathered parent material is sometimes found on the surface of eroded soils; conversely, dark topsoil is sometimes found plugging tunnels in weathered parent material at depths down to about a meter. There seems little reason to doubt that normally pocket gophers are a potent agent in soil formation.

The layer of rocks, usually coated with carbonate, which is found so often at the boundary between solum and weathered parent material (Fig. 10) is too common to be accidental, but it is not easily explained. One possibility is that the larger rocks have settled out of the solum over many centuries because of the ceaseless burrowing of pocket gophers. Another is that the position of the rocks may relate to the mechanics of soil creep. Opposed to the first explanation is the fact that pocket gophers do not burrow below the solum proper very much, so that it is hard to understand how they could cause rocks to settle out from the lower levels. Opposed to the second explanation is the fact that the rock layer is

often found where slopes are too gentle for creep to be important.

PRIMARY SUCCESSION

Two phases of primary succession will be considered, one on colluvial material and one on residual rock. The sites used as examples are selected, like the examples of climax or near-climax herbaceous vegetation that have been described, to avoid the influence of grazing by domestic livestock. Consideration is restricted to the xerosere, in consequence, for there are practically no examples of intermediate stages of the hydrosere in the subalpine zone of the Wasatch Plateau that have not been concentrated upon by livestock: wet meadows and the shores of streams and ponds are easily accessible to grazing animals, and are sought out for water and succulent forage.

In considering development of vegetation and soil the possibility must be conceded that many soils of the Wasatch Plateau are modifications under present-day climate of soils formed under materially different conditions. They may have begun to form during the Pluvial 20,000 or more years ago, or even earlier. If so, they would have been modified during the period of rising temperatures that is estimated to have begun some 9,000 years ago and ended perhaps 4,500 years ago (Antevs 1948), as well as by a climate fluctuating around the present level during the past 4,500 years. It is also possible, on the other hand, that many of the present soils of the subalpine zone have been formed during the past 4,500 years from the soft sedimentary rocks of the Wasatch Plateau. Paralleling the presumed history of soils, it is probable that spruce-fir forests were more extensive during cool, moist periods than they are today, and that they shrank during warm, dry periods, in which, doubtless, herblands became correspondingly more extensive.

Regardless of when and how the soils were formed, and of specific changes that the vegetation may have undergone, the essential fact to keep in mind is that post-Pluvial changes of soil and vegetation have evidently been orderly. During these many centuries vegetation and soil have maintained a balance while undergoing change. This fact is particularly impressive in the Wasatch Mountains of northern Utah, where the sandy beaches of ancient Lake Bonneville provide a record of equilibrium on steep watershed slopes that has persisted at least since the Pluvial. This equilibrium has been upset only in historic times (Bailey, Forsling & Becraft 1934).

Primary Sucession on Talus

Talus slopes and rock fields at the base of limestone cliffs provide, because of their inaccessibility, an excellent opportunity to observe initial stages of primary succession without complications from grazing by domestic animals. Rock chucks (*Marmota flaviventer*) and conies (*Ochotona princeps*) are the principal mammals of these talus slopes and rock fields. Only after the rocks are greatly decomposed, and the intervening spaces are filled with fragments and fine materials, do deer gain access to them, and ultimately livestock.

A striking fact about primary succession on these areas is the conspicuous invasion of trees—alpine fir and Engelmann spruce—as pioneers (Fig. 11). Trees invade regardless of exposure, although they are more numerous on north- than on south-facing slopes.

FIG. 11. Early pioneer stage in primary succession on limestone rock fields and talus. Trees are alpine fir and Engelmann spruce. Note young trees and shrubs in foreground. Some of the gravelly spaces between larger rocks in foreground support a sparse growth of herbaceous vegetation (Fig. 12). Head Twelvemile Canyon, west exposure, 10,100 ft. elev. F-443925

Shrubs are also likely to be present: *Ribes leptanthum, Lonicera involucrata, Salix* spp., *Sambucus racemosa, Pachistima myrsinites, Juniperus communis*, and, especially on dry sites, *Aplopappus macronema*. Most of these shrubs are present in the foreground of Fig. 11.

In pockets of gravelly soil the pioneers are forbs and grasses: *Agropyron trachycaulum, Trisetum spica-*

FIG. 12. Early pioneer stage in primary succession on a pocket of gravelly soil that has formed between large limestone blocks (Fig. 11): sparse, rather small forbs and grasses. The pinnate leaves of *Polemonium delicatum* are readily distinguishable. Erect *Agropyron trachycaulum* at left with spike silhouetted against rock is 53 cm tall. Low shrub at right is *Aplopappus macronema*. Head Twelvemile Canyon, west exposure, 10,100 ft. elev. F-443926

tum, Poa interior, Polemonium delicatum, Erigeron compositus, Anemone globosa, and *Synthyris laciniata.* All these species are present in Fig. 12, together with the shrubs *Aplopappus macronema* and *Ribes montigenum.*

On sites where shale is especially important in the parent material, although often the surface is covered with a layer of limestone fragments, one finds *Aquilegia coerulea* (much dwarfed), *Aster glaucodes, Senecio amplectens, S. fendleri, Silene petersonii, Calamagrostis scopulorum,* and *Arenaria nuttallii.*

Lichens and mosses are not conspicuous on these limestone rocks. The three commonest lichens are *Endocarpon* (*wilmsoides?*), *Lecidea* (*L. rivulosa* group), and *Caloplaca* (*C. elegans* group). *Grimmia commutata* is the commonest moss on dry sites, with *Tortula ruralis.* On moist sites, *Brachythecium collinum* is the commonest moss, and *Timmia bavarica* is found in shaded pockets. The fern, *Cystopteris fragilis* occurs in crevices on very moist exposures.

A later part of this pioneer stage is illustrated in Fig. 13. Here the smaller rocks are either decomposed or mingled with the soil that has formed between the large rocks still jutting out of the forest floor. The soil that has been formed is well protected from erosion by the heavy layer of gravel on the surface, a natural erosion pavement. The site is still dominated by forest; even the little opening in which the picture was taken contains many small spruces and firs which indicate that it will be overshadowed by trees in the future, as the decaying stumps and logs indicate that it has been in the past. The shrubs are:

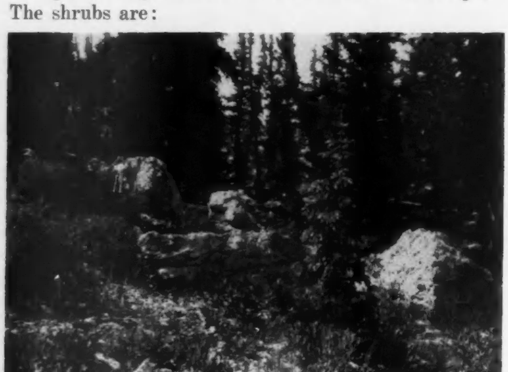

FIG. 13. Late pioneer forest stage in primary succession on a rock field at the base of a talus slope. Spaces between the large rocks are filled with gravelly, rocky soil which supports many tall mesic forbs and grasses. Several species of shrubs grow here. Trees are mostly Engelmann spruce with a few alpine firs. Old, decayed stumps show that this is not the first generation of trees to occupy the site. Head Twelvemile Canyon, west exposure, 10,000 ft. elev. F-464229

Ribes montigenum	*Lonicera involucrata*
R. leptanthum	*Rubus idaeus*
Salix sp.	*Juniperus communis*
Symphoricarpos oreophilus	

The principal forbs and grasses are:

Mertensia leonardi	*Achillea lanulosa*
Aster chilensis	*Senecio ambrosioides*
Bromus anomalus	*Fragaria bracteata*
Agropyron trachycaulum	*Polemonium delicatum*
Castilleja leonardi	*Thalictrum fendleri*
Penstemon subglaber	

Thus there is a mingling here of trees, shrubs, and forbs like Polemonium which characterize early pioneer stages, with tall, mesic species like Mertensia, Bromus, and Castilleja which characterize the climax herbaceous cover.

A more advanced stage, apparently intermediate in the course of primary succession, is one in which trees are scarce or absent and tall shrubs, with an understory of herbaceous vegetation, are abundant. The intermediate character of tall-shrub communities can be inferred from the facts first, that their soils, which may be deep, are usually full of rocks, and second, that they frequently occur in a transitional zone between herbaceous openings and coniferous timber. The herbaceous components of tall-shrub communities are essentially those of the upland-herb association, although, because these communities are usually found on warm, southerly exposures, there is a tendency toward the xerophytism found in limber-pine and erosion-pavement communities.

Two examples will be given in which the tall-shrub community is well along toward dominance by herbaceous vegetation. The first is on an easterly slope of 70% derived from limestone talus on Block Mountain. It has probably not been much affected by grazing. Although the soil is extremely rocky, fine, dark soil material is between the rocks, even at the surface. The proportions of vegetation, rock, and surface soil are 44, 52, and 4%, respectively, and therefore the surface, between foliage and rocks, is almost completely protected. Species, in abundance classes (p. 14), are as follows:

Ribes inebrians	4
Symphoricarpos oreophilus	3
Thalictrum fendleri	3
Mertensia leonardi	3
Lathyrus lanszwertii	2
Sambucus racemosa	2
Vicia americana	1
Agropyron trachycaulum	1
Bromus carinatus	1
Monardella odoratissima	1
Senecio ambrosioides	x
Stipa columbiana	x
Erysimum elatum	x
Smilacina stellata	x
Achillea lanulosa	x
Lonicera involucrata	x
Castilleja viscida	x
C. miniata	x
Epilobium angustifolium	x
Bromus anomalus	x
Festuca sp.	x
Ribes leptanthum	x
Descurainia richardsonii	x

Here tall shrubs make up 50% of the cover although, because they are somewhat taller than the herbaceous plants, they appear to be dominant. A number of species are common to the upland-herb association (Thalictrum, Mertensia, Vicia, Agropyron, Stipa, Achillea, *Bromus* spp.), with a few species belonging to timbered (Epilobium, Lonicera) and to dry, rocky sites (Monardella, *Castilleja viscida*).

The second example is from a southerly exposure of about 40% near the top of Black Mountain, where the vegetation is exposed to extreme drying not only from the direct rays of the sun all day, but also from the prevailing southwesterly wind. The soil is derived from limestone and is gravelly. On this slope are scattered patches of limber pine and a little aspen and alpine fir. Surrounding the stand to be described is an erosion-pavement community dominated by the following four species, and these indicate the xeric character of the site:

Lomatium nuttallii
Monardella odoratissima
Castilleja viscida
Eriogonum neglectum

The stand itself occupies about a quarter of an acre with cover as follows: vegetation 47.5, litter 25.0, rock 16.2, and bare ground 11.3%. The species in order of abundance are:

Symphoricarpos oreophilus	4
Agastache urticifolia	3
Helianthella uniflora	3
Ribes leptanthum	2
R. montigenum	1
Ligusticum porteri	1
Monardella odoratissima	1
Agropyron trachycaulum	1
Bromus carinatus	1
Melica bulbosa	1
Lathyrus lanszwertii	1
Osmorhiza occidentalis	1
Erigeron speciosus	x
Linum lewisii	x
Mertensia leonardi	x
Viguiera multiflora	x
Viola purpurea	x
Chenopodium album	x
Collomia linearis	x
Galium bifolium	x

This patch of vegetation has probably not been grazed by livestock although close utilization of Pachistima indicates that deer-use in this vicinity is heavy. Shrubs make up half the cover but they are low, and the aspect of the community is herbaceous. Some herbaceous species reflect the dry site—Agastache, Helianthella, Monardella, Linum, Viguiera, and Viola; but others are characteristic of much more mesic sites, notably Ligusticum, Osmorhiza, Erigeron, and Mertensia. A very few anuals are present. Notably absent are *Stipa lettermani* and *Taraxacum officinale,* which would be present and probably dominant on such a site if it were heavily grazed by livestock. Both species are dominant on more accessible grazed range on top of Black Mountain. *Artemisia discolor* is also conspicuously absent, although it would flourish on such a site.

The abundance of shrubs (39%) and rockiness of the soil of stand 935 (Table 7) on a steep northerly exposure at the head of Ephraim Canyon have already been noted. This one and stand 986 at the head of Twelvemile Canyon (shrubs 13%) probably represent a still more advanced stage in transition between the pioneer vegetation of talus slopes and the herbaceous climax. Tall shrubs are conspicuous in both, and in both the solum contains much skeletal material; yet the solum is so clearly distinct from underlying parent material (Fig. 10) that, on the basis of soil development, these two stands are apparently much nearer climax than pioneer vegetation.

Thus the pioneers in succession on warm, dry sites appear to be coniferous trees and shrubs in crevices, certain forbs and grasses in pockets of gravelly soil, and a few lichens and mosses on rock surfaces, the trend being toward dominance by conifers. The second major stage in succession in evidently one of dominance by tall shrubs, although in some instances this stage may be lacking. The third major stage is one of dominance by grasses and tall forbs. These relations are shown diagrammatically in Fig. 14. It will be well at this point to summarize the evidence. (In reviewing this the relation of plant communities

FIG. 14. Scheme of primary succession involving concurrent development of vegetation (left) and soil (right) on warm, dry sites. This succession begins on talus of limestone rock and culminates in the mixed upland-herb association.

to topography and soil, as illustrated in the Manti Canyon transect (Fig. 2) should be recalled. There, changes from steep to moderate slopes with corresponding changes from trees to herbaceous vegetation and from shallow to deep soils suggest the direction of succession.) The evidence may be arranged under seven heads:

1. Conifers, both Engelmann spruce and alpine fir, invade talus slopes and rock fields on warm, dry exposures. Tall shrubs invade similarly, but the trees tend to form a closed canopy and dominate the site as they increase, with shrubs, forbs, and grasses as an understory.

2. Conifers maintain dominance after a soil mantle is developed, mainly on north exposures. On south and west exposures with a well-developed soil mantle, conifers tend to be confined to moist, springy places. These facts suggest that the forest requires more water than the grassland. These forest soils are usually shallower and rockier than grassland soils. (The contrast between forest and grassland soils will be elaborated further when the spruce-fir association is taken up.)

3. On steep south exposures where slumping is common and the soil mantle is rocky, tall shrubs tend to be dominant. These soils seem to be intermediate in development between the very rocky soils of conifer-dominated talus and the nearly rock-free profiles of the upland-herb association. Areas on these south exposures dominated by grasses and forbs have soils less rocky than areas dominated by shrubs. Hence it would appear that shrubs ultimately give way to herbaceous vegetation when the slopes become stable.

4. On level areas or on moderate slopes, and associated with a rather deep, rock-free soil profile, one finds herbland. The greater depth of profile, together with the relative scarcity of rocks, indicate that succession has proceeded from conifer and shrub communities to a herbland community, and not the other way around.

5. Below many cliffs in the subalpine zone are narrow shelves or terraces. These appear to have been formed by fracturing and slipping of a slab of the underlying strata. Some rotation of the slab is involved, for commonly a ridge is formed parallel with the cliff and separated from it by a trough. The ridge is usually characterized by rock outcrops and is covered with spruce and fir; the trough is characterized by a deeper soil, and when this is the case it supports few trees and is dominated by herbaceous vegetation. Elsewhere, when the soil of the trough is very rocky, it is dominated by trees. These relations suggest that when soil has had a chance to develop in the trough it is occupied by herbaceous vegetation and reproduction of trees is prevented.

6. At the edges of warm, dry openings, like the Block Mountain natural area, conifers appear to be retreating. Decaying stumps and fallen trees outnumber the young trees becoming established. Generally conifer reproduction in upland-herb communities of the subalpine zone is not impressive, and is found mostly where the vegetal cover has been thinned and the soil bared. Aggressive tree reproduction does take place, however, chiefly in the stands of shrubs that dominate old burns on north exposures.

7. Like trees, tall shrubs do not invade grassland aggressively. They do invade where soil is being rapidly eroded, as shown by comparison with photographs made early in the process. They may also invade a dense herbaceous cover along the trunks of fallen trees and along the log fences of corrals and exclosures. These facts suggest that tall shrubs, like trees, are more demanding in their moisture requirements than herbaceous vegetation, at least for successful establishment.

On warm, dry sites it thus appears probable that, as soil development proceeds and the soil becomes deeper and less rocky, young conifers and young shrubs find it increasingly difficult to become established in competition with herbaceous vegetation. Some of the trees that die are not replaced, and presumably the same thing is true of the tall shrubs, so that eventually herbaceous vegetation reigns supreme. The presence of charred wood in the soil of certain herbaceous stands, as in the Block Mountain natural area, indicates that fire may be instrumental in hastening this succession.

Primary Succession on Residual Rock

The soil of the greater part of the subalpine zone, the slopes and drainage basins, is colluvial in origin, but that on ridges is derived from residual limestone or shale. Figure 15 shows an early stage in the process of development on limestone, and Fig. 16 a relatively mature profile. Both these profiles, from essentially level ground on Elk Knoll, are believed to have been affected but slightly by accelerated erosion.

In Fig. 15 a pavement of limestone gravel covers the surface. This gravel is in a matrix of grayish brown clay soil only a few centimeters deep. The organically darkened soil fills crevices in the limestone parent material to a depth of about 30 cm. At this depth organic soil in the crevices gives way to whitish clay. Jointed limestone bedrock is encountered at about 50 cm.

The soil surface and vegetation bear some resemblance to those of small, gravelly areas found in limestone talus (Fig. 12), although in this case the vegetation was probably modified by heavy grazing 50 years ago. Vegetation covers only about 10% of the surface. It is made up of the following species in the abundance classes indicated:

Lomatium nuttallii	4
Eriogonum neglectum	3
Orthocarpus tolmiei	3
Erigeron speciosus	3
Ligusticum porteri	2
Gilia pulchella	1
Agropyron trachycaulum	1
Stellaria jamesiana	1

FIG. 15. Profile of an immature soil under a heavy erosion pavement. Elk Knoll, head of Manti Canyon, 10,000 ft. elev. F-443905

FIG. 16. Profile of a relatively mature soil developed on residual limestone. Stand 971, Elk Knoll. See Fig. 9 for description. F-443902

Vicia americana	1
Viguiera multiflora	1
Thalictrum fendleri	1
Geranium richardsonii	x
Mahonia repens	x
Taraxacum officinale	x
Collomia linearis	x
Frasera speciosa	x
Rosa fendleri	x
Artemisia discolor	x
Monardella odoratissima	x
Astragalus carltonii	x
Viola purpurea	x
Trisetum spicatum	x
Stipa lettermani	x
Androsace septentrionalis	x

Dominance by Lomatium and Eriogonum and the presence of Monardella are reminiscent of the marginal, erosion-pavement community surrounding a natural area dominated by herbaceous species and shrubs on Black Mountain (p. 119). The presence of some forbs and grasses (Erigeron, Agropyron, Viguiera, Thalictrum) suggests the mixed upland-herb association. *Artemisia discolor* and *Stipa lettermani* probably reflect the influence of previous overgrazing.

The relatively mature soil pictured in Fig. 16 and described in Fig. 9, and the vegetation it supports, are at the other extreme. The vegetation of Elk Knoll, the 30-acre area surrounding it, is described in Table 12, and it will be sufficient here to list the most abundant species of the stand (No. 971, Table 9) in the immediate vicinity of the profile:

Erigeron speciosus	3
Aster foliaceus, A. chilensis	2
Penstemon rydbergii	2
Agropyron trachycaulum	2
Bromus anomalus	1
B. carinatus	1
Geranium richardsonii	1
Artemisia discolor	1
Melica bulbosa	1
Stipa columbiana	1
S. lettermani	1
Trisetum spicatum	1
Carex festivella	1
Achillea lanulosa	1
Erigeron ursinus	1
Frasera speciosa	1
Ligusticum porteri	1
Mertensia leonardi	1

Potentilla pulcherrima	1
Solidago ciliosa	1
Stellaria jamesiana	1
Valeriana occidentalis	1
Vicia americana	1
Eriogonum neglectum	1

The abundance of *Erigeron speciosus, Bromus* spp., Agropyron, Carex, Ligusticum, Mertensia, and Valeriana indicates a strong tendency toward restoration of the original upland-herb association. The abundance of Artemisia, *Stipa lettermani,* and a number of other low-growing or rhizomatous species (Penstemon, Achillea, Solidago, Eriogonum, *Erigeron ursinus*) is probably related to depletion of the vegetation by grazing prior to 1903.

There is evidence to suggest that tall shrubs play an intermediate role in the primary succession of vegetation on residual soils of ridges, as they appear to do on the colluvial soils of slopes. On certain knolls and ridges aerial photographs show a regular pattern of dark, circular spots, which, on the ground are found to be low mounds with a slight craterlike depression in the center. Such mound-patterns are strikingly like the patterns formed by tall shrubs, mainly *Ribes* spp., on other ridges. On a ridge in the northwest corner of Sec. 5, T18S, R5E these low mounds average 23 ft. in diameter and 57 ft. from center to center. Pocket gophers are more active in the soil of mounds than in the soil between mounds, which suggests that the soil of mounds is deeper.

Excavations in two localities revealed that soil of the mounds is indeed deeper. A trench dug across one mound showed that the rock-free topsoil was 41 cm deep on the average, and that it tapered away from the mound to an average depth of 20 cm. In the second locality the respective depths were 45 and 36 cm. A pit was dug in still another mound 23 m away and the solum was found to be 56 cm deep: halfway between the two mounds it was only 29 cm deep.

In the little flat where the shallow profile was dug (Fig. 15) there are some low, circular mounds like these, of deeper soil than prevails on the flat, covered by *Ribes montigenum.* This shrub has a tendency to layer. Its decumbent outer branches are often partly covered with winter earth cores by pocket gophers, and adventitious roots develop. In this way a single bush may spread outward, in time forming a hollow ring—for it dies out in the center —15 or 20 ft. in diameter. The soil surface tends to be slightly elevated under the shrubs and slightly depressed in the center, in the form of a shallow crater. The similarity in form and size of these mounds, together with their similarity in pattern of occurrence, suggests that mounds now free of shrubs were formerly occupied by them. The evidence therefore points toward succession on residual soils, as well as on colluvial soils, from tall shrubs toward a herbaceous climax. More work on this problem needs to be done before the transition can be described in detail.

What is the position of trees in successional development on residual soils? This is a difficult question primarily because on these level uplands there are no extensive areas of bare rock comparable to the talus that marks the beginning of succession on slopes: the soils are already well developed, and therefore examples of early stages are lacking. A suggestion is given, however, by the small spruce-fir patches that occur on some of these flat ridges. Because they are at the same topographic level, these timber patches appear to have arisen on the same kind of site as the surrounding herbland. Upon closer investigation one finds a rockier, shallower soil than that of the herbland. This difference in character of soil is illustrated by a pair of profiles on Toms Ridge (Fig. 17), one dug in a spruce-fir patch, the other in surrounding Stipa grassland a short distance outside. The patch is elliptical in outline, with axes of 18 and 20 m. Six spruces in it exceeded 200 years, three 300 years, and one with a rotten center was estimated to be close to 700 years of age. The two profiles were perhaps 75 m apart. For these profiles, organic-matter content was estimated simply by inspection, based on some familiarity with samples that had been analyzed from other profiles.

The differences in soil structure and color are marked, but the most obvious difference is one of depth, large rocks appearing in the 12-27 cm horizon of the forest soil, but at 40 to 66 cm in the grassland

SPRUCE-FIR PATCH	STIPA GRASSLAND
+15 cm.	
Duff Soil surface 0 cm.	Soil surface 0 cm.
Reddish brown clay loam; irregular nut structure to cloddy, friable; numerous roots, considerable gravel; perhaps 20% organic matter. −12 cm.	
Reddish brown clay between rock; cloddy; compact; numerous roots; perhaps 5% organic matter. −27 cm.	Grayish dark brown clay loam containing much limestone gravel throughout; fine crumb structure near surface grading into soft nut at depth; loose at surface to rather compact at depth; abundant roots; perhaps 8% organic matter. −50 cm.
Light buffy gray clay mixed with limestone rock and gravel; no evident structure; compact; a good many roots; probably less than 1% organic matter. Rocks in this portion of profile are the exact counterpart of parent material in grassland pit, but are much larger.	Pale buff or light buffy gray clay mixed with limestone rock and gravel; no evident structure; friable to compact; numerous roots; probably less than 1% organic matter.

FIG. 17. Comparison of two soil profiles, in spruce-fir patch and under adjacent grassland, Toms Ridge (T17S, R5E, S30; elev. 10,000 ft.). Horizontal solid lines indicate soil surface and division between solum and parent material; broken lines indicate top of duff and minor zonal division.

soil, and on the average at 50 cm. It was observed in the field that pocket gophers did a great deal to mix and aerate the grassland soil, and some of their tunnels, plugged with dark earth, were found to extend well into the C horizon. In contrast, there was no sign of pocket-gopher activity beneath the conifers. Presumably most of the mixing there is accomplished through the upcasting of soil by the roots of windthrows, certainly a much slower process. This difference in physical disturbance is doubtless one reason for the difference in soil depth.

The difference between these profiles throws light on primary succession. If the succession were from grassland to conifer forest, as Sampson (1919) suggests, one would expect the soil under conifers to be at least as deep as that under herbaceous cover. It is seldom so deep, however, and, as in this comparison, it is usually much shallower. If there is to be a replacement of one of these communities by the other under the existing climate, the soil profiles show that it cannot be replacement of grassland by conifer forest; it must be replacement of conifer forest by grassland. It seems reasonable to conclude, therefore, that this patch of spruce and fir originated in one of two ways, either through invasion of a rock outcrop by conifers, perhaps under a climate similar to the present one, or as part of an extensive conifer forest, perhaps in a moister climate, of which this patch and the many others like it in the subalpine zone are remnants, persisting on the rockier soils.

Thus, in a general way at least, and confining our attention to warm, dry sites, evidence for succession beginning on residual rock corroborates the evidence for succession beginning on talus. In both, a similar, well-defined and fairly rock-free soil profile supporting a herbaceous plant community appears to be climax, and the early stages in both are marked by very rocky substrata and dominance of trees or tall shrubs. More work needs to be done to solve such problems as the relation of spruce-fir patches to the tall-shrub and dark-spot patterns on ridges, and to erosion-pavement communities on shallow, residual soils.

Forb-Dominated Communities on Cattle Range

In a number of heavily grazed parts of the subalpine zone of the Wasatch Plateau, particularly in broad headwater basins, terraces, and ridges on the west side, one finds herbaceous communities dominated by such forbs as *Geranium richardsonii, Taraxacum officinale, Artemisia discolor, Achillea lanulosa,* and *Penstemon rydbergii.* Grasses are generally scarce, so that these forb-dominated communities contrast sharply with the grass-dominated communities that occur mostly east of the main axis of the plateau. The forb-dominated areas have been grazed by cattle for many years, while those dominated by grasses have been grazed by sheep.

There are of course other factors, particularly variations in site from place to place, that tend to obscure the effects of selective grazing. Making allowances for these, the evidence for the influence of cattle on plant composition will be derived from forage preferences of cattle, plant composition on comparable areas grazed to different degrees by cattle, and recorded vegetal changes under cattle grazing and protection.

SITE CHARACTERISTICS

Climate and soil of forb-dominated communities on cattle range are those of the original mixed upland-herb association, except as microclimate has been modified by changes in vegetal cover, and soil by accelerated erosion. In most essential respects there is no difference in the quality of site of cattle range as compared with sheep range. In one respect there is a material difference, and this results from an interaction between the grazing habits of the animals and topography. The most severely eroded cattle range is on low-lying, level ground where cattle tend to concentrate, avoiding steep slopes, whereas the most severely eroded sheep range is likely to be on sloping ground with its high erosion potential, or on ridges where sheep are commonly bedded.

There is considerable variability in the character of surface soil, part of which arises from differences in parent material and part from differing degrees of accelerated erosion. It is believed that the best index to fertility of these soils is given by their organic-matter content. With this, total nitrogen content and presumably other important factors, particularly soil aggregation, are closely correlated. In Table 4 the organic-matter determinations from range grazed strictly by cattle in recent years are those from Philadelphia Flat, Alpine Cattle-Pasture, and Carrying-Capacity Pasture. These values are obviously part of the general population and are in no way atypical.

VEGETATION

The two species that are most common throughout these forb-dominated communities on cattle range are *Geranium richardsonii* and *Taraxacum officinale.* Locally dominance may be shared by *Artemisia discolor, Penstemon rydbergii, Achillea lanulosa, Erigeron ursinus,* or *Aster chilensis.* Geranium and Taraxacum fruit freely and have impressive seed-dispersal mechanisms, which may account for their widespread occurrence. The other species are all rhizomatous. They flower later in the season (Fig. 7), and in years of early frost some of them may not produce viable seed. Seedlings of these rhizomatous species seldom appear on repeatedly charted, permanent quadrats, whereas seedling plants of Taraxacum and Geranium appear frequently.

Often one can recognize a sequence of ages, and hence infer invasion by these forbs into areas where the ground is bared and annual or early withering perennial species—which will be referred to collectively as "ephemerals"—are dominant. These ephemerals are principally *Polygonum douglasii, Collomia linearis, Madia glomerata, Viola nutallii, Claytonia lanceolata, Erythronium grandiflorum,* and *Stellaria jamesiana.*

On heavily grazed cattle range the rhizomatous species form well-defined patches, with the ground between patches dominated by ephemerals.

Where grazing pressure is less severe, as at greater distance from water or on steep slopes, one finds a more varied mixture of forbs and some grasses. The commonest species are *Erigeron speciosus, Valeriana occidentalis, Lupinus alpestris, Castilleja sulphurea, Ligusticum porteri, Stipa lettermani, Trisetum spicatum,* and *Agropyron trachycaulum.* These species increase and others come in under still lighter grazing by cattle. Specific examples of this gradation of species composition with grazing pressure will be described later.

THE GRAZING FACTOR

The most casual observer crossing the Wasatch Plateau near its center is impressed by the differences in herbaceous vegetation on the east and west sides. The heads of Ephraim and Manti Canyons on the west side are dominated my forbs, while the heads of Becks, Seely, and Bear Creek Canyons, and the intervening ridges on the east side, are dominated by grasses, chiefly *Stipa lettermani.*

The casual observer might suppose that the crest of the plateau acts as a barrier to rainfall borne on the prevailingly westerly winds, thus encouraging relatively xeric vegetation on the east side. In several years' field experience, however no such barrier effect has been detected. As an instrumental check, standard rain gages were set out during the summers of 1945 and 1946 in addition to two intensity gages regularly operated by the Intermountain Station, so that in all there were three gages on the west side in the head of Ephraim Canyon, one of which was practically at the summit, and two on the east side, in Horseshoe Flat and at the head of Seely Creek (Secs. 23 and 26, T17S, R4E). These gages were read weekly. They showed a great deal of variation from station to station for each weekly interval, as might be expected with summer storms in mountainous terrain. There was no consistency to these differences, however. The differences between stations on one side were of the same order as the differences between stations on different sides. Furthermore, variations tended to compensate, so that total seasonal precipitation was approximately equal at all stations. A clearer difference in precipitation than is shown by these measurements would be necessary to account for the marked differences in vegetation that exist.

The likelihood of a consistent difference in winter snowfall may also be ruled out. If such a difference did exist, it would have to be very marked to explain the differences in vegetation, for, as has already been pointed out, snow depth is so great in the subalpine zone that there is an excess of soil moisture on practically all sites each spring. Observations on several winter trips to the top of the plateau indicate that, although there is much local variation in snow depth, there is no consistent difference between east and west sides, except for a narrow strip in the lee of the plateau crest on the east side, where a deep snow cornice is formed each winter. This, however, is only a few yards wide, and has no bearing on the question of snow depth over vast acreages. For comparable drainage basins, the variation in snow depth between sites on either side appears to be greater than the variation between sides.

The difference in vegetation on the two sides of the main axis of the plateau is readily explained by differences in grazing use. Sheep were excluded from much of the west side of the plateau around the turn of the century because of the damage being done to village watersheds. Cattle had exclusive use of this range, therefore, for about 25 years. In view of the well-known differences in forage preference between sheep and cattle, it is probable that predominance of forbs on the west side is a result of suppression of grasses by cattle, while predominance of grasses on the east side is a result of suppression of forbs by sheep. This difference has persisted even though a partial exchange from cattle to sheep was made in certain westward drainages (e.g., Ephraim Canyon) about 1925.

There is considerable evidence to support this explanation. One bit is provided by the natural areas. Three of these (Ephraim Canyon, Black Mountain, and Twelvemile Canyon) are on the west side, one (Block Mountain) is on the east side. The vegetation on each is essentially similar, a mixture of tall forbs and grasses, but in each case this vegetation is markedly different from the low grasses on the east side and the low forbs on the west side. The vegetation on Elk Knoll, which has not been grazed heavily

TABLE 11. Percentage use of current vegetal growth by cattle near end of grazing season. Data from Philadelphia Flat are averages of observations made in 1938, '39, '42, '43, and '44; data for Carrying-Capacity Pasture are averages of different parts of the pasture in each year given.

	PHILADELPHIA FLAT		CARRYING-CAPACITY PASTURE			
	Center	West	1928	1929	1930	1931
Grasses and sedges						
Agropyron trachycaulum	87	74	73	60	55	58
Bromus carinatus	93	92	72	..	..	66
B. inermis	94	..	95	75	88	..
Poa pratensis	86	92	79	75	82	11
Stipa lettermani	62	52	72	75	42	36
Trisetum spicatum	33	34	3	15	20	..
Forbs						
Achillea lanulosa	28	26	T	5	4	..
Artemisia discolor	19	15	0	0	..	..
Aster chilensis	37	49	1	..	2	..
Geranium richardsonii	56	..	5	15	..	44
Ligusticum porteri	..	72	2	5	..	..
Penstemon rydbergii	10	17	T	15	6	1
Potentilla pulcherrima	28	42	50	..	..	..
Taraxacum officinale	79	79	20	30	8	11
Shrubs						
Sambucus racemosa	..	100	38	..	85	..

for about 50 years is also a mixture of grasses, sedges, and forbs, although grasses and sedges are virtually lacking on the heavily grazed cattle range around it. Finally, there are areas on the west side which have been trailed and grazed heavily by sheep. One of these is the ridge between the South Fork of Manti and the North Fork of Sixmile Canyons which has been used as a sheep driveway at least since 1910, and probably since grazing by livestock began. On this and some other areas grazed by sheep on the west side, *Stipa lettermani* is dominant, just as it is on the sheep range of the east side.

Forage Preferences of Cattle. Table 11 gives use data from cattle range on three sites and over several years. These figures represent the estimated percentages of total current growth removed by grazing. Philadelphia Flat was grazed all season long in the years of observation, while Carrying-Capacity Pasture was grazed for a relatively short period each year. Philadelphia Flat was also in poorer condition than Carrying-Capacity Pasture, supporting a much smaller volume of forage per acre, especially of grasses.

This table shows that cattle generally graze grasses more heavily than forbs. In general, too, use on Philadelphia Flat is considerably heavier than in the Carrying-Capacity Pasture. This heavier use is particularly marked with forbs, and it reflects the severer grazing and relative scarcity of desirable forage species on Philadelphia Flat.

Of the grasses in the table, Trisetum is least heavily grazed by cattle. It is rather generally present throughout the subalpine zone, but, despite preferential treatment, never dominates extensive areas as Stipa, Geranium, or Taraxacum do. Taraxacum is one of the forbs most readily grazed by cattle. Despite its relatively high palatability, Taraxacum is probably able to dominate overgrazed cattle range because of its early seasonal development, its appressed rosette (grazing-escaping) growth habit, and its rapid production of fruit. Sambucus is highly palatable in late summer or fall, when all the leaves are stripped from the stems, but is not grazed much until then. Probably the fact that it gets through most of the summer without being eaten accounts for its persistence and spread on overgrazed range.

The vegetal composition of heavily grazed cattle range tends to correspond inversely with the forage preferences of cattle. In general, grasses and sedges that are most heavily grazed by cattle tend to be scarce, while certain forbs that are less eagerly grazed are relatively abundant.

TRENDS UNDER CATTLE GRAZING

To demonstrate changes in vegetal composition caused by cattle grazing, three kinds of evidence will be presented, in addition to the inferences that can be drawn from forage preferences of cattle. First the vegetal composition of three rather extensive areas grazed to different degrees will be compared. Next, trends shown on permanent plots on cattle range will be examined. Finally changes on areas formerly grazed by cattle, but from which cattle have long been excluded, will be described using the evidence of permanent plots, range-survey records, and present-day observation.

A fact to be kept in mind is that these records begin *after* the vegetation had been greatly depleted and much soil erosion had occurred. On extensive areas perennial species had been destroyed entirely and replaced by ephemerals. It is very probable that by the time the first permanent plots were established some reinvasion of perennials had begun. The end result is not the direct effect of cattle grazing in changing composition of the original mixed upland-herb association, therefore, so much as its effect on composition of the vegetation replacing the ephemerals that became abundant after virtual denudation.

Vegetal Composition and Intensity of Grazing

The descriptions of stands on Elk Knoll, North Knoll, and Ridge in 1945 (Table 12) bring out differences between vegetation essentially ungrazed, moderately grazed, and heavily grazed, by cattle.

TABLE 12. Vegetal composition of three herbaceous stands under different intensities of grazing, head of North Fork of Manti Canyon, 1945. Elev. 10,000 ft. T18S, R4E, S3, 9, 10. Abundance symbols are explained on page 92.

Species	No grazing (Elk Knoll)	Moderate grazing (North Knoll)	Heavy grazing (Ridge)
Grasses and sedges			
Agropyron trachycaulum	2	2	x
Bromus anomalus	2	x	R*
B. carinatus	x	1	
Carex festivella	1		
C. hoodii	1	x	
C. raynoldsii	x		
Festuca ovina	R	R	R
Hordeum nodosum	..	x	
Melica bulbosa	2	1	R
Phleum alpinum	..	R	
Poa fendleriana	x	x	R*
P. palustris	x	x	R*
P. pratensis	x	x	x
Stipa columbiana	1	1	x
S. lettermani	1	1	2
Trisetum spicatum	x	x	x
Perennial forbs			
Achillea lanulosa	1	1	1
Agoseris arizonica	x		
A. pumila	x	x	1
A. taraxacifolia	R		
Aquilegia coerulea	x	R	R
Arabis lyallii	x		
Artemisia discolor	2	3	4
Aster chilensis, A. foliaceus	2	2	1
Astragalus carltonii	x	x	x
A. goniatus	..	..	x
Castilleja sulphurea	x	x	R
Crepis acuminata	x	x	
Delphinium barbeyi	x	x	x
D. nelsonii	R	x	1
Erigeron speciosus	3	3	2
E. ursinus	2	2	1

TABLE 12. (Continued)

Species	No grazing (Elk Knoll)	Moderate grazing (North Knoll)	Heavy grazing (Ridge)
Eriogonum neglectum	1	1	x
Erysimum elatum	x	x	x
Erythronium grandiflorum	x	x	x
Fragaria bracteata	..	x	
Frasera speciosa	x	1	x
Galium boreale	..	..	x
Geranium richardsonii	2	2	3
Gilia pulchella	x	x	1
Helianthella uniflora	1	x	R
Lathyrus lanszwertii	x	x	
L. utahensis	x		
Lesquerella utahensis	..	x	x
Ligusticum porteri	1	x	2
Linum lewisii	x		
Lupinus alpestris	x	x	1
Mertensia leonardi	1	R	
Oenothera flava	x	x	x
Osmorhiza occidentalis	x	x	R*
Penstemon rydbergii	1	3	R
Phacelia heterophylla	..	..	R
Polemonium foliosissimum	R	R	R
Potentilla glandulosa	x	x	R
P. pulcherrima	1	1	1
Pseudocymopterus montanus	R	x	x
Ranunculus inamoenus	R	..	1
Rumex mexicanus	x	x	
Senecio cymbalarioides	x	x	x
S. crassulus	1	x	1
Silene lyallii	x	x	x
Smilacina stellata	x	1	R
Solidago ciliosa	x	x	1
Stellaria jamesiana	1	x	x
Taraxacum officinale	x	x	1
Thalictrum fendleri	x	x	x
Thlaspi glaucum	..	..	R
Valeriana edulis	..	x	
V. occidentalis	x	x	
Vicia americana	1	1	1
Viguiera multiflora	1	x	R
Viola nuttallii	x	x	1
Annuals			
Androsace septentrionalis	..	..	R
Chenopodium album	x	x	x
Collomia linearis	x	x	x
Descurainia richardsonii	x	x	x
Orthocarpus tolmiei	1	1	1
Polygonum douglasii	x	x	x
Shrubs			
Artemisia tridentata	R		
Chrysothamnus nauseosus	..	..	R
C. viscidiflorus	x	..	R
Ribes inebrians	..	x	x
R. montigenum	x	1	
Rosa fendleri	x	x	R
Sambucus racemosa	x	x	x
Symphoricarpos oreophilus	x	..	x

*Indicates that plants are found only as relics in shelter of shrubs.

The proportions, in percent, that the four main classes of vegetation contribute to the respective totals are as follows:

	Elk Knoll	*North Knoll*	*Ridge*
Grasses and sedges	30	17	7
Perennial forbs	67	77	90
Annuals	2	3	2
Shrubs	1	3	1
	100	100	100

Clearly grasses and sedges decrease, and perennial forbs increase, with increasing cattle grazing.

The abundance symbols for most species of grass and sedge in Table 12 suggest a progressive decline with increasing grazing. The only species to show an increase under heavy grazing is *Stipa lettermani.* Fourteen species of grass and sedge are recorded on Elk and North Knolls, 10 on Ridge—and if those found as relics in the shelter of shrubs were to be excluded, there would be only 7.

Table 12 suggests that some forbs increase with increasing cattle grazing and that others decrease. The most clear-cut examples of those that increase are *Artemisia discolor* and *Delphinium nelsonii.* Others that are rather abundant and have a similar tendency are:

Geranium richardsonii	*Solidago ciliosa*
Agoseris pumila	*Taraxacum officinale*
Gilia pulchella	*Viola nuttallii*
Lupinus alpestris	

Several of these species are ephemeral or are notably abundant on accelerated-erosion pavement—Delphinium, Agoseris, Gilia, Taraxacum, and Viola. Less abundant species that are similar in association are:

Lesquerella utahensis	*Pseudocymopterus montanus*
Phacelia heterophylla	*Thlaspi glaucum*

Forbs showing the most clear-cut decrease with increasing grazing are *Helianthella uniflora, Mertensia leonardi,* and *Viguiera multiflora.* It is also notable that *Osmorhiza occidentalis* is listed on heavily grazed Ridge only as a relic.

Permanent Plots and Quadrats on Grazed Range

Storm's Plots: In 1919 Earl V. Storm laid out paired 10 x 10 m plots in various parts of the Wasatch Plateau. One plot of each pair was fenced and the other continued to be grazed. Three pairs (Gentry Mountain, T15S, R7E, S14; Cove Creek, T14S, R5E, S36; and Mount Baldy, T19S, R4E, S19) were located on cattle range in the subalpine zone. Cover and plant composition were determined in 1919, in one or more years in the period 1922-1925, and in one or more years in the period 1942-1946.

Unfortunately for our purpose the intensity of cattle grazing was not maintained, or some cattle were exchanged for sheep, so that details of trends under cattle grazing are obscured. The plots show clearly, however, that range overgrazed by cattle can be just as badly depleted as range overgrazed by sheep, and

TABLE 13. Average number of shoots per year on each of two meter-square quadrats on Philadelphia Flat, in four periods, 1916-48. (T17S, R4E, S34. Elev. 10,000 ft.)

	QUADRAT 23, UNGRAZED				QUADRAT 24, GRAZED			
	'16, '19, '22	'24, '27, '29, '32	'34, '35, '36, '38	'39, '40, '41, '43, '48	'16, '18, '19, '22	'24, '27, '29, '32	'34, '35, '36, '38	'39, '40, '41, '43, '48
Agropyron trachycaulum	0	1	138	187	..	..	..	..
Other grasses*	..	T	..	T				
Achillea lanulosa	90	124	54	112	71	102	124	108
Geranium richardsonii	2	6	12	25	0	0	T	0
Oenothera flava	3	2	1	T	1	0	0	0
Potentilla pulcherrima	..	..	..	..	T	1	4	8
Ranunculus inamoenus	25	6	2	4	2	4	T	2
Stellaria jamesiana	20	1	4	3	12	10	16	8
Taraxacum officinale†	25	37	63	52	38	78	72	123
Vicia americana	42	30	21	9	4	6	T	2
Viola nuttallii	37	72	52	76	24	32	34	45
Other perennial forbs‡	102	12	8	15	T	0	9	1
Chenopodium album	27	11	2	10	1	0	0	0
Collomia linearis	9	210	103	124	0	T	T	0
Descurainia richardsonii	11	6	1	8	23	2	1	0
Polygonum douglasii	258	76	74	220	140	24	253	154
Other annuals**	47	2	2	0	T	10	1	0

*Other grasses:
Poa reflexa (23)
Stipa lettermani (23)

†Seedling plants excluded.

‡Other perennial forbs:
Agoseris pumila
Arabis lyallii (23)
Aster chilensis (23)
Chaenactis (?) sp.
Claytonia lanceolata
Delphinum nelsonii (23)
Erythronium grandiflorum (23)
Penstemon rydbergii (23)
Rumex mexicanus (24)

**Other annuals:
Androsace septentrionalis
Lepidium sp.

that, in comparison with their decline on range heavily grazed by cattle, grasses and sedges increase under protection. It is also notable that *Artemisia tridentata*, a dominant on semi-arid lowlands which had not been present at the earlier examinations, was aggressively invading two of the three sites by the 1940's.

Philadelphia Flat: Quadrat 24 is on level, heavily grazed cattle range. Its soil, most of which is exposed to the elements because of scanty vegetal cover, has been greatly eroded in the past, although at present little erosion appears to be taking place. The organic-matter content of the surface inch, as determined in 1940, is 4.4 percent.

Quadrat 24 has been charted 17 times between 1916 and 1948. The summary of those records (Table 13), giving average numbers of shoots in four periods, shows the meager character of the cover and very little change during these 32 years of record. No grasses have been noted on the quadrat at any time. Annuals, mainly Polygonum, have always been abundant. Taraxacum and Viola have increased over the years. Potentilla has increased mostly by the tillering of one plant present in 1916, although one additional plant invaded between 1936 and 1938 and has persisted.

Quadrat 23 is nearby, on similar ground, but inside a log-and-block exclosure. Unfortunately the soil of this exclosure is repeatedly and thoroughly overturned by pocket gophers, and anything like a normal trend in recovery is obscured by this recurring disturbance. The surface soil shows a consistently lower organic-matter content than soil outside the exclosure. The lower percentage in the exclosure is attributable to pocket gophers' continually bringing subsoil to the surface, for there is no such consistent difference inside and outside large protected areas where no difference in pocket-gopher population is evident.

The effect of this continual disturbance is reflected in the abundance and persistence of annuals, particularly Polygonum, Collomia, and Chenopodium, and in the persistence of the ruderals or near-ruderals Taraxacum, Oenothera, and Viola. Despite severe disturbance the vegetation of the enclosed quadrat has improved materially as compared with the vegetation of the grazed quadrat, in that Agropyron has become a conspicuous component. The sudden drop in Stellaria after the first period, and the consistently fewer dandelions on the enclosed quadrat, may well be a result of foraging by pocket gophers. Underground parts of both species are abundant in some gopher caches.

The difference in Geranium between these two quadrats is not significant. There is the same amount of Geranium on a grazed 10 x 10 m major plot (No. 15), outside the exclosure, as on the ungrazed major plot (No. 2) inside.

The major plots corroborate the quadrats. Grasses are scarce on the grazed plot, averaging less than one percent of the cover, whereas in recent years (1940-48) grasses average 12% of the cover on the

enclosed plot. Taraxacum has been a consistent dominant on the grazed plot, averaging 60% of the cover since the first examination in 1922. Finally, as on the quadrat heavily grazed by cattle, the vegetation of the larger plot has changed very little in the 26 years of record.

Quadrat 25, in the middle of Philadelphia Flat, was originally protected in a large exclosure, but has been grazed for many years. It is better watered than most quadrats, sometimes being flooded until early summer, which may account for the relative luxuriance of its vegetation in spite of heavy grazing. On this quadrat Agropyron and the unpalatable Hordeum have increased greatly, although they are still only minor constituents of the cover (Table 14).

TABLE 14. Average number of shoots per year on one meter-square quadrat on Philadelphia Flat, in two periods, 1916-1948. (T17S, R4E, S34. Elev. 10,000 ft.)

	QUADRAT 25, GRAZED	
	1916, 1919	1940, 1941, 1943, 1948
Agropyron trachycaulum	T	164
Hordeum nodosum	0	154
Phleum pratense	0	1
Pca pratensis	6	7
Achillea lanulcsa	110	146
Aster foliaceus, Erigeron ursinus	212	464
Oenothera flava	8	5
*Taraxacum officinale**	30	33
Viola nuttallii	3	20
Other perennial forbs†	2	8
Chenopodium album	557	0
Collomia linearis	18	42
Descurainia richardsonii	4	4
Polygonum douglasii	250	120
Other annuals‡	0	T

*Seedling plants excluded.
†Other perennial forbs: *Agoseris pumila, Claytonia lanceolata, Plantago tweedyi, Rumex mexicanus, Stellaria jamesiana.*
‡Other annuals: *Androsace septentrionalis, Rorippa (?).*

The continuing abundance of Taraxacum, Viola, Polygonum, and Collomia indicate the continuing influence of heavy grazing and trampling, and, together with the slow spread of rhizomatous species, the slowness of change in dominance.

The invasion of ephemeral communities on heavily grazed cattle range by sod-forming, rhizomatous species, which this quadrat reflects, is one of the clearest evidences of secondary succession in the subalpine zone. The sod-forming species, particularly *Penstemon rydbergii, Artemisia discolor, Erigeron ursinus, Aster foliaceus,* and *A. chilensis,* are slow to invade, but are very persistent once they become established. *Achillea lanulosa* is also a member of this group, but is less persistent in the form of a well-defined mass.

Figure 18 shows an old and a young plant of Penstemon separated by the bare ground characteristic of the ephemeral community in late summer.

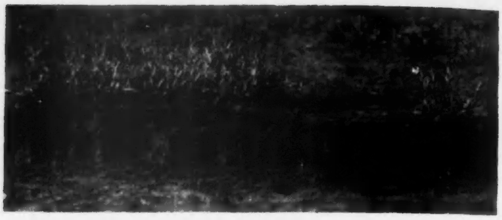

FIG. 18. An old and a young plant of *Penstemon rydbergii,* showing soil deposition and erosion. Soil level at time when older plant became established is shown by white string. Philadelphia Flat, August 28, 1946. F-443920

The white string, at the level of the root crown of the older plant, marks the original soil level. A maximum of 6 cm of soil has been deposited above this level, and a maximum of 6 cm of soil has been eroded from the bare space between the plants. In the crown of the younger plant 4 cm of soil has accumulated; the root crown of the younger plant is only slightly higher than the general level. The accumulations of soil may be from wind-blown particles, but the bulk of it here is probably from winter earth cores of pocket gophers.

While it is impossible to estimate the absolute ages of these rhizomatous plants in years, it is quite feasible to assess their relative ages, which is sufficient to establish the successional trend. The evidence includes: (1) size of plants, the younger being smaller; (2) habit of plants, the younger being more nearly circular in outline and of greater compactness and height; and (3) lesser pedestaling of the smaller plants by erosion of adjacent bare soil—that is, height of pedestaling tends to be proportional to age of plant. This kind of evidence regarding invasion by rhizomatous species may be observed widely in the subalpine zone today, corroborating and extending the evidence of their spread given by range-survey descriptions and permanent plot records.

The slowness of spread of most rhizomatous species is impressive. A permanent plot of 3,000 sq m was established on Philadelphia Flat in 1943 to study the invasion of *Madia glomerata* and the spread of Penstemon and Artemisia. The greater part of the plot is dominated by ephemerals—Polygonum, Collomia, Madia, Viola, Claytonia, Stellaria, etc., and the cover they provide is so scanty that the surface is essentially bare most of the summer. Most of the Penstemon and Artemisia patches appear to have increased in the 3-year interval, 1943-46, although the gain is so small that it may be a result of mapping error rather than growth. The 10 x 10 m grazed major plot No. 15 on Philadelphia Flat was mapped in 1940, 1946, and 1948. In the 8-year interval the outlines of Penstemon masses have changed very little. Changes in area of Penstemon and Aster have also been observed to be very slow on a number of permanent meter-square quadrats in the subalpine zone.

Trends with Grazing Removed

The foregoing evidence has shown that heavily grazed cattle range is dominated by perennial forbs and ephemeral species, and that little change takes place beyond the slow invasion of turfy, rhizomatous species to replace ephemerals. This vegetation, furthermore, is accordant with the forage preferences of cattle in that certain mesic grasses and forbs, which are eagerly grazed by cattle, are scarce or absent on such range. It will be of interest to note successional trends where sizable blocks of former heavily grazed cattle range have been protected.

Carrying-Capacity Pasture: Certain highlights in the succession of vegetation in this 6½-acre pasture have been given as evidence of trend toward a mixed grass-forb community after grazing has been reduced. These trends will be considered in more detail here.

Although sheep grazed and trampled the area very heavily prior to 1903 or 1905, use was probably by cattle from about 1903 until 1926, when the fence now enclosing this pasture was built. Between 1926 and 1937 grazing was more or less intermittent by horses and by overflow cattle or sheep from nearby experimental pastures. No regular grazing treatment was applied. Notes kept on utilization by cattle in 1929, 1930, and 1931 show that use was fairly heavy, particularly of grasses (Table 11). However, because of the intermittent character of use, the period between 1926 and 1937 can be considered fairly safely to have been a relief from the severe overgrazing of former years. Since 1937 no grazing has been permitted.

Seven permanent quadrats were established in 1913. Two were denuded to study reinvasion of vegetation. Subsequent charts indicate that the effects of denudation were overcome in from 6 to 10 years, a conclusion that has also been reached from study of similarly denuded quadrats on sheep range. This does not mean that the original, pristine vegetation can be restored in so short a time (it certainly cannot); it means only that the vegetation of the adjacent community comes to dominate the denuded square meter in that time.

When the 5 undenuded quadrats were established in 1913, the cover was very patchy, elevated masses of vegetation alternating with bare depressions. The dominant species were low and rhizomatous: *Poa pratensis, Penstemon rydbergii, Achillea lanulosa, Aster chilensis* and *Erigeron ursinus*, for the most part. The character of vegetation and surface soil are well portrayed in photographs made at the time, which show them to be essentially like cover and surface soil on parts of certain heavily grazed cattle ranges today. Much bare ground was exposed, and it was hard and caked. Pavement gravel was exposed on the surface of some quadrats, and on nearly all quadrats the depressed open spaces bore witness to sheet erosion (Fig. 19, Ellison 1949a, Figs 6 to 9).

The appearance of the quadrats has changed. The soil is no longer compact, but loose, except as bare spaces are washed and crusted after prolonged rains.

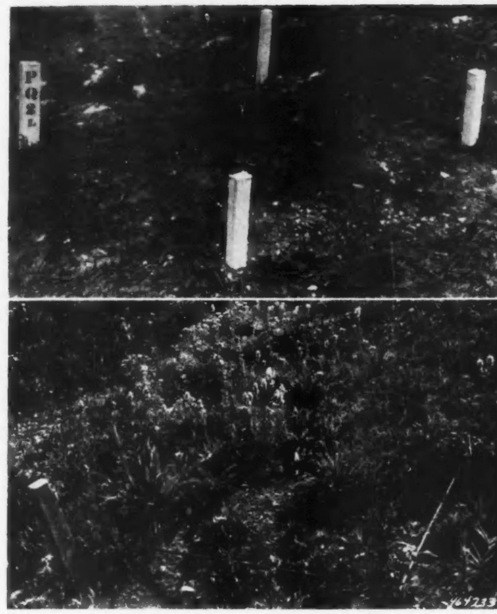

FIG. 19. Carrying-Capacity Pasture Quadrat 2 in 1913 (above) with scanty, low cover of Penstemon and Achillea, and in 1947 with taller, more varied vegetation including Penstemon, Aster, Achillea, Valeriana, Solidago, Gilia, and Castilleja. F-415548, F-464233

Vegetal cover is still far from complete, and some erosion is continuing on most of the quadrats. The vegetation is taller, partly because it has not been grazed for several years, but mostly because taller-growing species have invaded. Among the rhizomatous species *Poa pratensis* and Achillea have declined in abundance, although on some quadrats these species have maintained themselves fairly well. Penstemon has decreased on three quadrats, maintained itself on one, and increased on one. *Erigeron ursinus* has tended to maintain itself or increase. *Solidago ciliosa* and *Aster chilensis* have increased rather strongly.

Species composition of the quadrats has been materially enriched, from an average of 12.5 species per quadrat in 1913 to 21.5 species in 1948, an average increase per quadrat of 9 species in the 35-year period. The species may be grouped into rough classes based upon growth form and the kind of sites in which they are most commonly found. Most of those in the rhizomatous class have already been listed. Among non-rhizomatous species, the mesic group includes:

Aquilegia coerulea	*Lupinus alpestris*
Bromus carinatus	*Thalictrum fendleri*
Erigeron speciosus	*Valeriana edulis*
Geranium richardsonii	

The intermediate (between mesic and xeric) group includes:

Agropyron trachycaulum
Castilleja sulphurea
Melica bulbosa
Potentilla pulcherrima
Senecio integerrimus
Tristetum spicatum
Viguiera multiflora

The xeric group, of species common on warm, dry sites or erosion-pavement areas, includes:

Arabis lyallii
Erysimum elatum
Gilia pulchella
Lesquerella utahensis
Pseudocymopterus montanus
Silene lyallii
Stipa lettermani
Thlaspi glaucum

The ruderal and near-ruderal group includes:

Agoseris pumila
Oenothera flava
Plantago tweedyi
Ranunculus inamoenus
Rumex mexicanus
Taraxacum officinale
Viola nuttallii

Finally, the annual group includes:

Androsace septentrionalis
Chenopodium album
Collomia linearis
Lepidium densiflorum
Orthocarpus tolmiei
Polygonum douglasii
Descurainia richardsonii

On the average quadrat the number of species in each of the rhizomatous, mesic, intermediate, and xeric groups has increased by about two. The number of species in the ruderal and annual groups has not changed materially.

In terms of numbers of individual plants, annuals have decreased markedly. Ruderals and near-ruderals have never been abundant, and have not changed greatly over the years. Numbers of plants of most other species tabulated above have increased.

The quadrats may be classified, from most mesic to most xeric, on the basis of exposure and degree of erosion. (It must be understood that these terms are only relative; the quadrats represent varying samples of the "average" site rather than the full range between possible extremes.) With this classification numbers of annuals in early chartings may be correlated: there were many annuals on the mesic quadrats, fewer on the intermediate quadrats, and least on the xeric quadrats. Invasion of xeric and mesic species (as listed above) has followed the same pattern in recent years: virtually no xeric species on the mesic quadrats, few mesic species on the xeric quadrats. Thus these quadrats, even though they embrace only a small segment of the gamut of site conditions in the subalpine zone, clearly reflect site selectivity in the establishment of invading species.

The importance of microenvironment to establishment of subalpine vegetation has been demonstrated (Ellison 1949a), part of the evidence having been derived from these quadrats. This evidence consisted of the occurrence of new plants within established masses of vegetation much more frequently than in adjacent, sizable openings. Supplementary evidence indicated difference in character of microclimate—rather than in soil, rodent disturbance, etc.—to be the most important factor. It is interesting to note that the more xeric species seem to be affected by microclimate just as greatly as the more mesic species, for new plants of Pseudocymopterus, Lesquerella, Gilia, and other xeric species occur much more commonly within or adjacent to masses of established vegetation than they do in open spaces. In other words, even xeric species are more likely to become established on relatively mesic microsites than they are on open ground nearby. Having become established, they tend to work out into openings gradually.

These quadrat records emphasize the slowness with which natural revegetation proceeds and the fact that accelerated soil erosion on most of them is still taking place. It is probable that continuing erosion and slowness of vegetal invasion are reflections of the very great deterioration in soil and depletion of vegetation that had occurred before the pasture was fenced. If the quadrats were on particularly severe sites this continuing deterioration might not seem so remarkable, but the quadrat sites are fairly representative of moderate, southwesterly exposures. Indeed, a 1 x 2 m quadrat that is still eroding has a northwesterly exposure. If the cover were showing unqualified improvement one would expect invasion by mesic, or mesic and intermediate, species only. The fact that xeric species have been invading the quadrats only during the latter half of the period of record, and since the area was fenced, indicates something of the site deterioration that is taking place under virtually complete protection.

Since this range had been grazed by cattle for several years, it might have been expected that most native grasses would increase under protection. Agropyron has appeared on the quadrats on which it was not originally present and has increased on all of them. Bromus, Melica, Trisetum, and Stipa have also appeared and increased on certain quadrats. The most pronounced increase in grasses, and indeed, of other invading vegetation, took place after the pasture was fenced. But the grasses—except for Stipa on the driest and most actively eroding quadrats—appear to have reached a maximum between 1941 and 1943, and now seem to be declining. In 1948 one 1 x 2 m quadrat was dominated by Agropyron and Bromus, the grasses forming 37% of the total cover. On the other four quadrats, however, grasses made up substantially less than 10% of the cover in 1948, and on two of these, less than 5%. One may conclude, therefore, that, although grasses may have been released when grazing by cattle was removed, they show no tendency toward ultimate dominance, except perhaps locally.

Alpine Cattle-Pasture: An 80-acre area in the head of Ephraim Canyon was fenced in 1923 and was used in a cattle experiment between that date and 1937. Grazing by cattle, which varied somewhat in intensity from year to year, was based upon a carefully calculated grazing capacity, and was evidently materially lighter than grazing of the outside range. Sheep were grazed in the pasture in 1939, but in 1938 and each year since 1939 no grazing has been permitted except for a few saddle horses in late fall.

The information gathered in connection with the grazing experiment includes detailed range surveys in 1926, 1929, and 1932, charts of 11 permanent, meter-square quadrats established in 1925, and cover estimates of 11 5 x 5 m major plots also established in 1925.

The 1926 range-survey map, shows the dominance of two species, ***Penstemon rydbergii*** and ***Artemisia discolor***, in most of the herbaceous types. At present these species are still abundant, but they share dominance with a number of others, particularly *Erigeron speciosus* and *Valeriana edulis*. The grazed range to the west of the pasture, on the terraces lying above Philadelphia Flat, is overwhelmingly dominated by Penstemon today; and Erigeron, Valeriana, Castilleja, and other species that the records show to have increased in the pasture, are relatively scarce there. These cattle-grazed terraces, in other words, provide a picture in 1953 of the herbaceous vegetation of the Alpine Cattle-Pasture in 1923-26.

Let us consider the most evident changes in types No. 1 and 5, for which range-survey write-ups were made in July 29, 1947. Type No. 1 (3.48 acres) was designated "3-*Penstemon rydbergii-Stipa lettermani*" in 1926. Penstemon has made up about half the cover in all descriptions. Stipa, however, rose from 12% in 1926 to 17 or 18% in 1929-32, and has since declined to 5%. *Artemisia discolor* dropped from 10 to 3% of the cover in the 21-year interval. There have been two notable invasions: *Bromus anomalus* which was first noted in 1947, and *Erigeron speciosus* which increased from about 1% in 1926 to 20% in 1947. The type today would certainly be designated "3-*Penstemon rydbergii-Erigeron speciosus*."

In 1926 type No. 5 (6.49 acres) was called "3-*Penstemon rydbergii-Achillea lanulosa*." Penstemon, which made up 50% of the cover in 1926, has maintained its dominance, but Achillea has declined from 20 to 1%, and would certainly not be included in a type designation today. The proportions of Stipa and Artemisia have decreased essentially as they have on type No. 1. A number of species have increased in proportion, notably *Erigeron speciosus*, *Melica bulbosa*, and *Castilleja sulphurea*. *Bromus carinatus* and *Valeriana occidentalis* were first noted in this type in 1947.

Still another herbaceous type (type 12) has undergone an interesting change. In 1926 type 13a (0.22 acre) was broken out of type 12 (5.78 acres) which surrounded it, mainly because it was dominated by *Lupinus alpestris*. Today the two types are so much alike that they would not be separated. Lupinus is still overwhelmingly dominant in type 13a, but it has become a codominant, with *Erigeron speciosus*, in type 12. The percentages of these species in type 12 in 1926, 1932, and 1947 are as follows:

	1926	*1932*	*1947*
Lupinus alpestris	T	1	12
Erigeron speciosus	T	1	15

This increase in poroportion is consistent with other evidence of change in this pasture.

Two kinds of invasion have been taking place in the Alpine Cattle-Pasture in recent years. The first is an invasion of ephemeral communities by more persistent perennials. As on the grazed range (e.g. Philadelphia Flat), the rhizomatous forbs *Penstemon rydbergii* and *Artemisia discolor* are among these invaders. Nonrhizomatous perennial invaders include: *Ligusticum porteri*, *Geranium richardsonii*, *Senecio crassulus*, *Thalictrum fendleri*, *Viguiera multiflora*, and, in particularly sharp contrast to invasion on heavily grazed range, *Erigeron speciosus*, *Valeriana edulis*, *Agropyron trachycaulum*, and *Bromus carinatus* (Fig. 20). The evidence for inferring invasion of nonrhizomatous but persistent perennials includes a series of size classes and erosion levels; these indicate a series of age classes. Previous denudation of the area is attested by the existence of a general level populated with ephemerals and greatly subject to erosion.

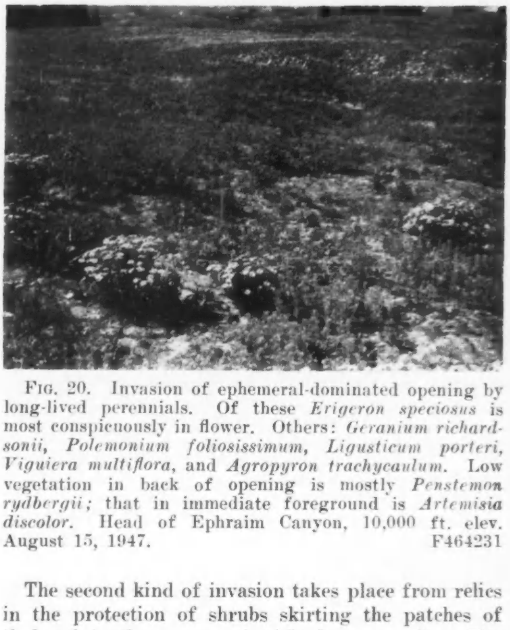

FIG. 20. Invasion of ephemeral-dominated opening by long-lived perennials. Of these *Erigeron speciosus* is most conspicuously in flower. Others: *Geranium richardsonii*, *Polemonium foliosissimum*, *Ligusticum porteri*, *Viguiera multiflora*, and *Agropyron trachycaulum*. Low vegetation in back of opening is mostly *Penstemon rydbergii*; that in immediate foreground is *Artemisia discolor*. Head of Ephraim Canyon, 10,000 ft. elev. August 15, 1947. F464231

The second kind of invasion takes place from relics in the protection of shrubs skirting the patches of timber into the open, upland-herb community. The evidence here is simply a radial progression of successively smaller (i.e., younger) plants from the edges of the timber outward. This kind of invasion is particularly easy to infer with *Mertensia leonardi*, *Polemonium foliosissimum*, *Osmorhiza occidentalis*, and *Valeriana occidentalis*. This observable evidence is supported by the fact that these species are now present in from 2 to 6 vegetal types in which they were not noted in one or the other of the early range surveys. Here, then, is another link in the chain of evidence that the upland-herb association was originally more mesophytic than it is today, with these tall forbs as conspicuous components; and that the present, prevailingly xeric character of the vegetation is a consequence of overgrazing.

The 11 meter-square permanent quadrats were evidently intended to be comparable when they were initially established, for they were similar in that each was dominated by *Penstemon rydbergii.* As on the Carrying-Capacity Pasture quadrats, but in lesser degree, the species composition of these quadrats has been enriched from about 12 species per quadrat in 1924 to over 15 in 1946. Most of this increase took place during the first few years after the pasture was fenced; the present trend is upward but is more gradual. The greatest increases have been of species in the rhizomatous and mesic classes. A summary of the most significant increases is given in Table 15.

TABLE 15. Number of quadrats out of 11 on which certain species occurred in the Alpine Cattle-Pasture at examinations made from 1924 to 1946.

	1924	1926	1929	1932	1934	1935	1936	1946
Geranium richardsonii	2	2	3	3	3	3	4	5
Erigeron speciosus	..	1	1	1	2	2	2	3
Artemisia discolor	..	..	..	1	3	2	2	3
Lathyrus lanszwertii	..	..	..	1	1	1	1	2
Castilleja sulphurea	..	..	..	..	..	..	..	1
Valeriana edulis	..	..	..	..	..	..	..	6
Orthocarpus tolmiei	..	..	..	..	..	..	..	7

Mesic species are Geranium, Erigeron, Lathyrus, Castilleja, and Valeriana. The spread of the rhizomatous Artemisia, as in the case of the Carrying-Capacity Pasture quadrats, probably relates to the introduction of this species on heavily overgrazed range many years before the pasture fence was built. The recent appearance of Orthocarpus is not understood beyond the fact that Orthocarpus, which forms sheets of yellow bloom in the head of Ephraim Canyon today, tends to occur on rather sparsely vegetated range, often in association with Artemisia.

The invading plants have in many instances increased in number. For example, *Erigeron speciosus* which appeared on quadrat U2 in 1934 with 3 shoots (having invaded some time between 1932 and 1934), increased to 43 shoots in 1946. On quadrat U3 there were 10 shoots of Erigeron in 1926, but by 1946 there were 621, and this species is now clearly dominant on the quadrat.

Other species on these quadrats have not changed greatly, increasing in some years, decreasing in others, without evident trend. One would naturally expect grasses (which were certainly suppressed by cattle grazing before 1923, just as they are suppressed today on comparable outside cattle range) to increase strongly when grazing pressure was lightened or removed. Such an increase has occurred, but it has been almost entirely in *Agropyron trachycaulum* between 1924 and 1932, and since 1932 there has been little change. The grasses, Agropyron, *Stipa columbiana, S. lettermani,* and *Trisetum spicatum,* have simply fluctuated, so far as the quadrat records go, at about a dead level, much as they have in the Carrying-Capacity Pasture. There is some indication that *Melica bulbosa, Bromus anomalus,* and *B. carinatus* have increased in the Alpine Cattle-Pasture, but they are as yet all minor species, and the increases are local.

GRASS-DOMINATED COMMUNITIES ON SHEEP RANGE

The communities included under this head occupy the ridges and headwater basins east of the axis of the plateau, for the most part. More precisely, they correspond with those parts of grazing allotments in the subalpine zone that have been heavily grazed by sheep for many years. The reason they occur mostly on the east side of the plateau is that sheep were pretty generally confined there, until about 20 years ago, by exclusion from the west side during the early 1900's.

As in the case of forb-dominated communities on cattle range, grass-dominated communities on sheep range are primarily a result of selective grazing. Speaking very broadly, grasses are less palatable to sheep than forbs, and, under heavy utilization by sheep year after year, forbs are handicapped and grasses are favored. Hence in time forbs tend to disappear and grasses come to dominate the stand.

This explanation is an oversimplification, as, indeed, the term "grass-dominated community" is. Actually forage preferences are only part of the explanation of trends. Certain rhizomatous forbs, *Achillea lanulosa, Artemisia discolor, Erigeron ursinus,* and *Penstemon rydbergii,* are codominants in some of these "grass-dominated" communities, partly because they are only slightly or moderately palatable to sheep, no doubt, but also because their rhizomatous growth habit enables them to store food reserves out of reach of grazing animals and to make rapid regrowth after having been grazed, if moisture and warmth allow. *Taraxacum officinale,* which does not have rhizomes, is also a common codominant of grasses in these communities. The disadvantage of a relatively high palatability in its case appears to be offset by phenological and morphological adaptations, for it flourishes under heavy grazing by sheep or cattle.

SOIL

The soil characteristics of these communities are those of the soil under the original mixed upland-herb association. As with forb-dominated communities on cattle range, the chief differences in depth result either from thinning of the soil profile by accelerated erosion or, in some places, of deepening by accelerated deposition. As on cattle range, too, much of the variation in character of surface soil is a result of variation in erosion.

As Table 4 shows, organic matter content may be less than 2% (upper Bear Creek). Here on a slope of 20%, topsoil has been completely eroded and

the surface sample is taken from what is really subsoil. (The dominant plant here is *Agropyron trachycaulum*, known from plot records to have invaded since 1916.) At the other extreme, on a stable, level, well-aggregated soil on Becks Ridge two miles to the north, organic matter is as high as 6.7%. This range is dominated by needlegrass (*Stipa lettermani*) and other grasses.

Many of these upland-herb communities have been invaded by yellowbrush (*Chrysothamnus viscidiflorus*) with the result, apparently, that organic-matter content of the surface soil is increased. The soil at Lower Horseshoe, for example, dominated by yellowbrush and needlegrass at the present time, has an organic-matter content of 6.8%. The surface soil of another yellowbrush-needlegrass community on Wagon Road Ridge, which has been under protection for almost 35 years, contains 6.6% organic matter (Table 4). These rather high values for organic matter, as compared with most others in this table, are not so much a reflection of some quality of yellowbrush *per se* as they are a reflection of an approach to normal soil stability which yellowbrush on these two sites helps to achieve. In support of this inference it will be recalled that the Elk Knoll and Twelvemile profiles (Fig. 9), of soils that appear to be normally stable under herbaceous cover, have organic matter contents in the 0-10 cm level of about 8%.

From these observations it may be concluded that these grass-dominated communities are not limited in their extent by soil fertility. They occur on very fertile soils in excellent tilth and on severely eroded soils sadly lacking in structure. Grasses—*Agropyron trachycaulum, Bromus carinatus, Stipa lettermani*—are usually among the earliest invaders on the raw surfaces of roadbanks, fills, and natural landslips, and are usually the first persistent perennials to invade harsh, eroded soils dominated by *Madia glomerata*.

VEGETATION

The cover of these grass-dominated communities is highly variable. On level stretches with low erosion potential and where soil is deep, well-dispersed vegetation may cover more than 65% of the surface. On slopes, however, individual plants are usually spaced far apart, covering as little as 10 or 20% of the total surface. The tendency for herbaceous plants, particularly grasses, to be pedestaled above the general level on such sites bears witness to active accelerated erosion. The Bear Creek quadrats provide examples of this condition.

There are at least 6 rather well defined aggregations of plants that fall into the class of grass-dominated communities on sheep range. These are:

1. *Stipa lettermani* and *Taraxacum officinale* dominant. This is the most common and widespread aggregation (Fig. 21). Most of the evidence of change presented in this paper on the basis of permanent plots involves this community. The plots and quadrats in Becks Creek, Becks Ridge, head of Seely

FIG. 21. Close-up of heavily grazed sheep range dominated by *Stipa lettermani* and *Taraxacum officinale*. As the exposed bare surfaces and tendency toward pedestaling suggest, this particular cover is not dense enough to protect the soil. Head of Ephraim Canyon, July 22, 1948. F-464237

Creek (in part), Toms Ridge, Erosion Areas A and B (in part), and Wagon Road Ridge (in part) sample it.

2. *Agropyron trachycaulum* dominant. This grass, a prominent constitutent of the original mixed upland-herb association, is a conspicuous dominant on eroded areas along the axis of the plateau. It invades road fills and abandoned roads. The community it dominates bears some relation to the foregoing in that Agropyron is sometimes codominant with Stipa. The Bear Creek plots and quadrats fall in this community.

3. *Agropyron subsecundum* and *Elymus salina* dominant. This community occurs on the easternmost tops of dry ridges, such as Wagon Road Ridge. It is similar in appearance, and is probably a more xeric counterpart, of the community dominated by *A. trachycaulum*.

4. *Hesperochloa kingii* dominant. This community occurs on windswept ridges that are practically denuded of topsoil. The dense bunches of Hesperochloa, which sometimes occur on hummocks of wind-blown soil, usually alternate with areas of erosion pavement that support typical erosion-pavement species, or some of the more xeric species of the upland-herb association. The Hesperochloa community occurs on high, exposed parts of Wagon Road Ridge and Cove Mountain. A curious feature of the larger bunches of Hesperochloa, which have dead centers and are horseshoe-shaped, is that the opening in the horseshoe is always on the leeward (east or northeast) side. The grass on the convex, windward side of the bunch is taller and thicker than the rest, and one gets the impression that the bunches are advancing into the wind, capturing wind-blown soil particles from the interspaces, disturbed by the trampling of sheep, on their windward side.

5. *Agropyron dasystachyum* (or A. *riparium*—there is some doubt as to the identity) dominant. This rhizomatous grass forms sod patches in several places

in the subalpine zone. What is perhaps the largest such patch is pictured by Sampson (1919, plate II) occurring on Buck Ridge. Very little besides the dominant grass grows in these stands, partly because of the competitive powers of the wheatgrass, perhaps, but also because sheep tend to eliminate other, more palatable species. This community was considered by Sampson to be one phase of the climax herbaceous vegetation of the subalpine zone. For reasons already given I consider this interpretation incorrect.

6. Small mat-formers dominant. One of these is *Carex eleocharis*. Another is *Muhlenbergia richardsonis*. These communities are of little importance; they are small and occur infrequently. Because of their rhizomatous, sod-forming habit, these species appear to be ecological counterparts of *Agropyron dasystachyum*. Like *A. dasystachyum* they demonstrate that under severe grazing rhizomatous species are much more effective than bunchgrasses in checking soil erosion.

THE GRAZING FACTOR

General observation shows that sheep prefer certain species of forbs to most grasses and often graze around grasses in selecting forbs to eat. Exceptions to this rough rule have been discussed already, and it should also be pointed out that forage preferences vary considerably with time of year, character of season, composition of the stand, and handling of the animals. *Stipa lettermani* for example, may be grazed early in spring before the fruits have developed, and again in fall if the herbage is softened by rain or if more palatable forage is gone. When sheep are being trailed, too, they appear to graze indiscriminately on species of all degrees of palatability, as compared with their highly selective habit of grazing when they are undisturbed. It should not be assumed that there is always a known reason for these variations in preference. In some years sheep may pass by the same plants they graze closely in other years, for no apparent reason. These variations make it impossible to define forage preferences precisely.

Some descriptions of grazing use in different places at different times will serve to show the species usually preferred and avoided by sheep, and also something of the way that preferences vary from year to year.

In a grazing use study on Toms Ridge in 1942, plots were clipped on grazed and protected range, both before and after sheep grazing. Production and consumption of forage were thus ascertained directly, in terms of weight. It was found that grasses, mainly *Stipa lettermani*, were used only 16%. Forbs, however, were used much more heavily, ranging from 34% for *Artemisia discolor* to 98% for *Erigeron ursinus*. Table 16 gives the results in detail and shows that use of certain species is out of all proportion to their abundance. Thus, of grass, which produced 632 pounds of herbage, only 101 pounds were eaten, while of the 44 pounds of herbage produced by Erigeron, practically all (43 pounds) was eaten.

TABLE 16. Consumption by sheep of herbage in an upland-herb community dominated by *Stipa lettermani*. Toms Ridge (T17S, R4E, S36, elev. 10,000 ft.), 1942. Weights are of air-dry herbage.

Species	Production lbs./acre	CONSUMPTION lbs./acre	CONSUMPTION percent
Grass, mainly *Stipa lettermani**	632	101	16
Taraxacum officinale	273	164	60
Penstemon rydbergii	207	84	41
Artemisia discolor	116	39	34
Achillea lanulosa	92	52	57
Erigeron ursinus	44	43	98
Viola nuttallii	23	13	57
Agoseris pumila	12	10	83
Vicia americana	9	5	56
Polygonum douglasii, *Thalictrum fendleri*, *Smilacina stellata*, *Androsace septentrionalis*, *Potentilla pulcherrima*, *Collomia linearis*, *Pseudocymopterus montanus*, *Ranunculus inamoenus*, *Lepidium* sp., *Lesquerella utahensis*, *Delphinium nelsonii*	6	4	67
Total	1,414	515	36

*Detailed estimates in 1944 showed *Stipa lettermani* to make up 85.0% of the grass by weight, *Trisetum spicatum* 7.2, *Agropyron trachycaulum* 4.3, *Stipa columbiana* 3.0, *Hordeum nodosum* 0.4, and *Poa pratensis* 0.1%.

On August 7, 1945, shortly after sheep grazed the area, 24 species in a certain depleted upland-herb community (T18S, R4E, S3, 10,300 ft. elev.) were grouped into four preference classes on the basis of volume grazed, as follows:

60-100% grazed
Agoseris pumila
Delphinium barbeyi
Ligusticum porteri

20-40% grazed
Erigeron ursinus
Geranium richardsonii
Oenothera flava
Pseudocymopterus montanus
Taraxacum officinale

1-20% grazed
Achillea lanulosa (inflorescences)
Agropyron trachycaulum
Artemisia discolor (inflorescences)
Aster chilensis
Astragalus carltonii
Poa nevadensis
Rumex mexicanus
Stipa columbiana (leaves only)
S. lettermani (leaves only)
Trisetum spicatum
Viola nuttallii

Not grazed
Festuca ovina
Lesquerella utahensis
Polygonum douglasii
Ranunculus inamoenus
Thalictrum fendleri

The grasses were among the plants least grazed. It is notable, too, that in grazing grasses sheep often select leaves and avoid flower heads, whereas in grazing certain forbs they eat flower heads and fruit.

This fact may also help explain why forbs tend to decrease on sheep range, and grasses to increase.

Observations on grazing use by sheep (dry ewes) were made in a 9-acre pasture at the head of Ephraim Canyon during early July in 1946 and 1947. This was early enough in the season so that the animals had considerable freedom of choice and were not forced by necessity to graze the more unpalatable species. On the basis of extent of use the species were tabulated in four preference classes in each of the two years: "preferred," "secondary," "little grazed," and "not grazed."

Species in the two higher preference classes both years were:

Agoseris pumila	*Ranunculus inamoenus*
Castilleja sulphurea	*Rumex mexicanus*
Erigeron speciosus	*Solidago ciliosa*
Ligusticum porteri	*Taraxacum officinale*
Mertensia leonardi	*Valeriana edulis*
Polemonium foliosissimum	*V. occidentalis*
Potentilla pulcherrima	*Vicia americana*
Pseudocymopterus montanus	*Viola nuttallii*

Included in this list are some of the tall, mesic forbs that are scarce on most sheep range, notably Castilleja, Erigeron, Ligusticum, Mertensia, Polemonium, and the two species of *Valeriana.*

Species in the two lower preference classes both years were:

Artemisia discolor	*Ribes inebrians*
Festuca ovina	*R. montigenum*
Lesquerella utahensis	*Sambucus racemosa*
Thalictrum fendleri	

The four herbaceous species tend to be abundant on sheep range. If the area had been grazed in late summer or fall instead of spring, the three shrubs (and *Chrysothamnus viscidiflorus,* which was classified as "secondary" one year and "little grazed" the other) would doubtless have been taken more eagerly.

The grasses:

Agropyron trachycaulum	*Stipa columbiana*
Poa fendleriana	*S. lettermani*
P. palustris	*Trisetum spicatum*
P. pratensis	

were classified as "little grazed" in 1946, but in 1947 Agropyron was classified as "preferred" and the other 6 species as "secondary." The reason for such relatively high preference for grasses is twofold. First, grasses are usually grazed more readily in spring than later in the season. Second, in 1947 the sheep were put in the pasture when vegetation was less well developed by 3 or 4 weeks than it had been in 1946, so that grass foliage was exceptionally young and tender.

The general tendency for sheep to prefer certain forbs to most grasses is evident from all these observations. This tendency is strong enough so that it cannot be obscured either by differences in plant composition from stand to stand or by differences in season of grazing, although it is clear from the variations in preference that both factors influence the selection of forage by sheep.

TRENDS UNDER SHEEP GRAZING

The forage preferences that have been described provide a suggestion of trends in vegetal composition under sheep grazing. Other and more substantial evidence will be drawn from the composition of stands that have been heavily grazed by sheep for many years in comparison with stands on natural areas and stands grazed by cattle; the presence of relic species on sheep range; changes in composition shown by range-survey records; and trends observed on permanent plots and quadrats.

Comparative Composition

Differences between the vegetation of sheep range and that of comparable range which has never been grazed by domestic livestock, or grazed only occasionally or lightly, give a measure of the change that sheep grazing has caused.

Table 17 shows considerable variation between three stands on sheep range. The species that tend to be most abundant in stand 984 are *Stipa lettermani* and *Agropyron trachycaulum* among the grasses, *Achillea lanulosa, Aster chilensis,* and *Erigeron ursinus* among the rhizomatous forbs, and *Taraxacum officinale* and *Pseudocymopterus montanus* among the palatable but early-maturing, taprooted forbs. In addition *Rudbeckia occidentalis* and *Sambucus racemosa,* which are not grazed until fall, and *Lathyrus lanszwertii,* which is little grazed at any time, are especially abundant.

The Block Mountain natural area, which is separated from nearby grazed range by steep, densely timbered slopes, cliffs, and talus accumulations of large limestone blocks, provides an opportunity for comparison. Differences in composition between stand 983 of the natural area and stand 984 on the grazed range may be studied by comparing tables 7 and 17. The following species are markedly less abundant on the grazed than on the protected range:

Mertensia leonardi	*Delphinium barbeyi*
Erigeron speciosus	*Ribes montigenum*
Heracleum lanatum	*Symphoricarpos oreophilus*

Mertensia, Erigeron, and Heracleum, which are highly palatable to sheep, have unquestionably been eliminated from stand 984 by grazing. Delphinium has probably been reduced by grazing (and probably the less abundant *Aster engelmanni* and *Lupinus foliosus* also), but because these species are marginal associates of timber they may be unduly abundant on the natural area. For this reason, too, it is doubtful whether the difference in abundance of the shrubs Ribes and Symphoricarpos is significant.

At the same time the following species are markedly more abundant on the grazed range:

Rudbeckia occidentalis	*Aster foliaceus*
Achillea lanulosa	*Erigeron ursinus*
Stipa spp.	*Chenopodium album*
Agropyron trachycaulum	*Polygonum douglasii*
Taraxacum officinale	*Sambucus racemosa*

Stipa, Taraxacum, Achillea, Rudbeckia, and Agropyron are among the most widespread and abundant plants on heavily grazed sheep range in the subalpine zone, and it may be concluded that sheep grazing has encouraged them. This is also true of the annuals Polygonum and Chenopodium. Since these rhizomatous species of Aster and Erigeron and the shrub Sambucus do not reproduce aggressively by seed, differences in their abundance may relate to accidents of distribution.

A similar comparison may be made between the sheep range of Swedish Knoll (stands 979, 980, Table 17) and Elk Knoll (Table 12) which has been protected from severe grazing for about 50 years. The sheep range has more grass than Elk Knoll, but it is lacking in ***Bromus anomalus*** and ***Melica bulbosa*** which are evidently palatable to sheep. The two bluegrasses, *Poa fendleriana* and *P. palustris*, occur only as relics under shrubs on the sheep range.

The sheep range is notably lacking, too, in the following forbs:

Erigeron speciosus	*Eriogonum neglectum*
Geranium richardsonii	*Orthocarpus tolmiei*
Mertensia leonardi	*Stellaria jamesiana*
Senecio spp.	*Artemisia discolor*
Helianthella uniflora	*Aster foliaceus*
Viguiera multiflora	*Erigeron ursinus*
Ligusticum porteri	*Penstemon rydbergii*

The species in the left column have probably been suppressed by sheep grazing. This is indicated by parallel evidence near Block Mountain or their occurrence as relics on sheep range, as well as the palatability of most of them to sheep. The case for the species on the right column is less strong: their relative scarcity may be due to chance. This is almost certainly true with *Artemisia discolor* which is abundant on much heavily grazed sheep range.

Species that are comparatively abundant on the grazed range include:

Achillea lanulosa	*Lesquerella utahensis*
Stipa lettermani	*Taraxacum officinale*
Pseudocymopterus montanus	

There is a resemblance here to the equivalent list from stand 984 near Block Mountain.

If one compares stands 979 and 980 on sheep range with the vegetation of like sites on cattle range (North Knoll, Ridge, Table 12) he finds similar differences.

Evaluating smaller differences by noting their consistency in all these comparisons, it will be found that the following additional species are suppressed on sheep range:

Agoseris spp.	*Lupinus* spp.
Aquilegia coerulea	*Osmorhiza occidentalis*
Castilleja spp.	*Potentilla glandulosa*
Crepis acuminata	*Silene lyallii*
Erysimum elatum	*Valeriana occidentalis*

TABLE 17. Vegetal composition of three herbaceous stands on heavily grazed sheep range.† Abundance symbols are explained on page 92.

Stand No.	984	979	980
Aspect	NE	..	..
Percent Slope	20	0	0
Vegetation, percent	37	23	19
Litter, percent	12	22	11
Bare ground, percent	51	55	70
Grasses			
Agropyron trachycaulum	2	1	3
Bromus carinatus	1		
Carex festivella	1	x	
Festuca ovina	..	..	R
Hordeum nodosum	..	..	1
Poa fendleriana	..	..	x*
P. palustris	..	..	x*
P. pratensis	x	1	
Stipa columbiana	1	..	x
S. lettermani	3	5	1
Trisetum spicatum	..	1	
Perennial forbs			
Achillea lanulosa	2	3	4
Agastache urticifolia	x		
Aplopappus integrifolius	..	..	x
Artemisia discolor	..	x	x
Aster chilensis, A. foliaceus	1	x	1
Astragalus carltonii	..	..	1
Clematis hirsutissima	..	..	x
Delphinium barbeyi	x		
Erigeron ursinus	1	1	1
Frasera speciosa	..	..	x
Geranium richardsonii	..	..	R
Helenium hoopesii	x		
Lathyrus lanszwertii	3		
L. utahensis	..	..	x*
Lesquerella utahensis	..	1	2
Ligusticum porteri	..	..	x*
Oenothera flava	x		
Osmorhiza obtusa	x	..	x*
Penstemon subglaber	..	..	x*
Polemonium foliosissimum	..	..	x*
Potentilla pulcherrima	x	x	1
Pseudocymopterus montanus	..	1	3
Ranunculus inamoenus	x	x	x
Rudbeckia occidentalis	4		
Rumex mexicanus	..	x	
Senecio ambrosioides	x		
Solidago ciliosa	..	x	
Stellaria jamesiana	x		
Taraxacum officinale	2	1	1
Thalictrum fendleri	1	2	x
Thlaspi glaucum	..	x	x
Valeriana occidentalis	x*		
Vicia americana	x	..	1
Viola nuttalli	x		
Annuals			
Androsace septentrionalis	x	x	x
Chenopodium album	1	x	
Descurainia richardsonii	x		
Lepidium sp.	x		
Polygonum douglasii	1		
Shrubs			
Chrysothamnus viscidiflorus	..	..	x
Ribes inebrians	..	..	x
R. montigenum	x	..	x
Sambucus racemosa	3		
Symphoricarpos oreophilus	..	..	x

†Stand 984. Head of Muddy Creek, 9,700 ft. elev., T20S, R4E, S9.
Stand 979. Near Swedish Knoll, 10, 200 ft. elev., T18S, R5E, S2.
Stand 980. Near Swedish Knoll, 10,200 ft. elev., T18S, R5E, S2.

*Relics: Plants found only in shelter of shrubs.

Most of these species are palatable to sheep. Similar differences among certain ephemerals (*Delphinium nelsonii, Erythronium grandiflorum, Collomia linearis*), the rhizomatous *Smilacina stellata* which does not appear to spread aggressively by seed, and *Delphinium barbeyi* which also tends to be localized, are judged to be of doubtful significance.

Thus the composition of stands heavily grazed by sheep is markedly different from comparable stands that are either ungrazed or that are grazed by cattle. The differences correspond inversely to the forage preferences of sheep: those species most relished by sheep tend to be abundant on natural areas and many of them are present on cattle range, yet they are absent from comparable heavily grazed sheep range. The inference follows that grazing by sheep has suppressed them.

Relics

A significant relic that has frequently been found on overgrazed sheep range is the roots of *Geranium richardsonii* preserved in the soil. The plants are dead and the roots are badly decayed, but there can be no question as to their identity, for a complete series, from decayed roots through sound but dead roots, to roots of living plants, has been obtained. These relic roots have been found on Toms Ridge and on Buck Ridge in the stand of *Agropyron dasystachyum* considered by Sampson to be climax and pictured by him (1919, plate II). That this Geranium should have been so completely suppressed bespeaks the severe grazing that this subalpine sheep range has suffered, because Geranium is not usually considered a very palatable species. At present Geranium and some other forbs, notably *Erigeron speciosus*, appear to be begining a slow reinvasion of some sheep ranges.

Living plants occur as relics in inaccessible places, particularly inside the thorny shelter of Ribes bushes. Among plants relished by sheep, which may sometimes be found in these sheltered places, are *Poa fendleriana, Castilleja leonardi, Osmorhiza occidentalis, Ligusticum porteri, Heracleum lanatum, Mertensia leonardi*, and *Polemonium foliosissimum.* The epithet "relished" is hardly applicable to *Aquilegia coerulea* and *Geranium richardsonii*, except on ranges that have been very greatly depleted, but on sheep ranges of the subalpine zone of the Wasatch Plateau, these species, too, are often found as relics in the shelter of shrubs.

These species are palatable to sheep, at least in comparison with more abundant plants on the range; they are scarce or absent on accessible parts of heavily grazed sheep range, but common on comparable natural areas; and one of them, Geranium, is very abundant on comparable cattle range. Putting these facts together, one is led to the conclusion that these species are vestiges of a former vegetation that was more mesic than the open-growing, herbaceous vegetation of today, and that heavy sheep grazing has caused the change.

Range-Survey Records

A comparison of range-survey write-ups made in the period 1912-1914 with those in the period 1936-38 shows that a number of major changes took place during the 23-year interval. These changes are partly the result of grazing pressures during the interval itself, but perhaps even more the result of invasional processes set in motion prior to 1912. Denudation of the original cover and baring of the soil set the stage for invasion, not only of some foreign weeds, but also of certain native species.

The general use of range-survey records has been described under "Methods of Study." The areal extent of types in which certain species were found, and the proportion of cover that each species made in its type, have been taken from type maps and field descriptions and recorded on semitransparent overlays. We thus have two related bases for judging change—change in areal extent of types, and change in proportion of species within types.

As an example of the method, consider Figure 22, on which the outlines of those types containing *Artemisia discolor* have been combined for each sur-

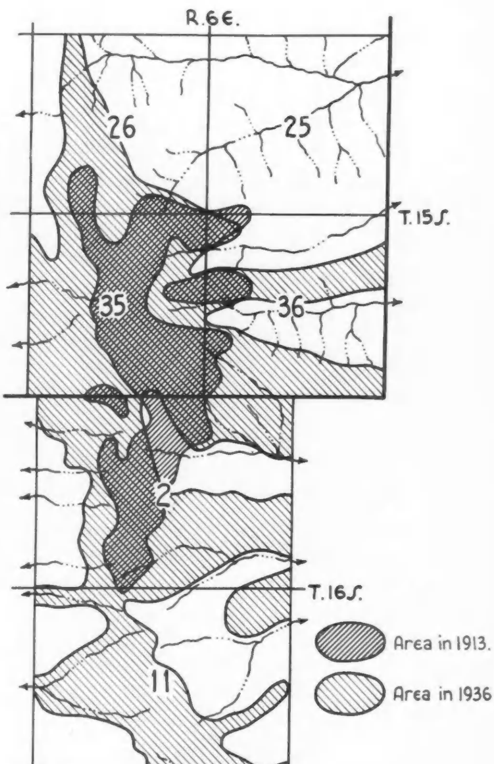

FIG. 22. Occurrence of *Artemisia discolor* on 6 sections on East Mountain in 1913 and 1936, according to range-survey forage type descriptions. The upper four sections are each about one sq. mi., the lower two 1½ sq. mi., in area. Elev. 9,500-10,500 ft.

vey. First it will be seen that Artemisia has increased greatly, from types totaling 470 acres in 1913 to types totaling 2,370 acres in 1936. The proportions made up by Artemisia are not shown, but to illustrate what is meant, the elliptical area that in 1913 lay on the ridge running from section 35 to 36 may be considered. In 1913 14% of the vegetation in this type was Artemisia. In 1936 the enlarged area was broken into two types, that to the west containing 44% Artemisia, that to the east containing 1½%. Since the type containing 44% in 1936 corresponds roughly in section 36 with the type containing 14% in 1913, and taking into account the enlarged area of Artemisia at smaller percentages, it is concluded that the proportion of Artemisia has increased in the vegetal cover of the section as a whole.

Type maps covering some hundreds of land-survey sections, wholly or partly within the subalpine zone, have been examined by each criterion. The data for 6 species are summarized in Table 18. To illustrate the significance of these figures, consider them for *Artemisia discolor*. Of the 228 sections on which identification of Artemisia was reasonably certain, 180 showed an increase in area, 15 a decrease, and 33 little change. Changes of this species in the vegetal composition of the 228 sections followed a similar pattern. It will thus be seen that Artemisia, Taraxacum, Chrysothamnus, and Helenium have all increased strongly, both in terms of areal distribution and percentage composition. The changes in Symphoricarpos and Thalictrum, however, are not well marked by either criterion, and therefore, there is no reason to believe that these two species have increased or decreased materially.

TABLE 18. Numbers of land-survey sections showing change in area and proportion for six species, between 1912-14 and 1936-38 range-surveys.

	CHANGE IN AREA			CHANGE IN PROPORTION		
	Increase	Decrease	Doubtful	Increase	Decrease	Doubtful
Artemisia discolor	180	15	33	185	17	26
Taraxacum officinale	252	25	62	272	19	48
Chrysothamnus viscidiflorus	169	12	43	153	43	28
Helenium hoopesii	89	3	35	78	21	28
Symphoricarpos oreophilus	119	53	162	143	57	134
Thalictrum fendleri	24	47	49	33	48	39

Of the four species in Table 18 that have clearly increased, Chrysothamnus will be considered in some detail later. It is appropriate here to consider some of the factors in the spread of the other three.

Figure 22 illustrates the process of invasion by *Artemisia discolor*. Artemisia occurred in 1913 principally on ridges—the areas from which soil is most severely eroded by sheep in grazing, bedding, and trailing. The extensions of area between 1913 and 1936 were also on ridges and on south-facing slopes—open, herbaceous types for the most part, readily denuded by overgrazing. If the percentage composition of Artemisia in the individual types could be shown in Figure 22, it would be seen that the greatest percentages in both surveys occur on the central portion of the main ridge, and become progressively less northward, southward, and to each side. This also suggests that Artemisia first invaded the central portion and has since spread outward. Range-survey data from many other places in the subalpine zone corroborate this pattern of spread.

Artemisia discolor is usually associated with eroded surfaces—that is, with past overgrazing. It is perhaps more correct to say that this species is associated with denudation of cover, even on areas that are not materially eroded. For example, on Toms Ridge (T17S, R4E, S25, 36, 10,000 ft. elev.) it grows in a concentric band around each of several spruce-fir patches where sheep seek shade during the heat of the day. The dominance of annual weeds in some of these places indicates the denudation and soil disturbance they undergo, and these factors, plus the probability that sheep introduce the seed, give a reasonable explanation for the invasion of Artemisia.

Although it is often associated with sheep grazing, *Artemisia discolor* is one of the dominants on range grazed solely by cattle during the last 50 years, such as the head of Manti Canyon. An old photograph shows it to have been well established here in 1910, so it may have been introduced by sheep before they were excluded in 1903.

The fact that this Artemisia is absent from large areas in the subalpine zone also bears upon the problem of its origin and spread. The southern end of the plateau is rather generally free of it, although a small patch has been observed in one eroding slope at the head of Gunnison Valley (S14, T20S, R3E), and it is evidently invading parts of the headwaters of Muddy Creek (T19, 20S, R4E) along roads and sheep trails. The eastern ends of some of the longer ridges are also free of it. On Wagon Road Ridge, for example, it has been observed as far east as S7, T18S, R5E, but no farther, although there are many eroded surfaces where it will readily grow. In these examples it seems clear that Artemisia has not yet had sufficient time to spread from the central and northern parts of the plateau, either southward or eastward, as far as it will ultimately go. Furthermore, all the natural areas but one (Table 7) are free of it. It is possible that seed may have been washed down from heavily grazed range above this area, or that sheep may have introduced it on the slope itself 50 years ago.

The evidence for invasion of ephemeral communities by rhizomatous species like *Artemisia discolor* and *Penstemon rydbergii* has already been mentioned (Fig. 18 and related text). It happens that these two species are extraordinarily persistent under heavy grazing and on terrain where erosion is rapid. With their rhizomatous growth form they would have persisted, had they been present, while bunchgrasses and taprooted forbs were being eliminated by extreme overgrazing. If they had been part of the original

vegetation, in other words, they should be well distributed today, having held their ground while other members of the upland-herb association were being destroyed. Because they are obviously *invading* extensive areas dominated by ephemerals, however, one is led to doubt whether either of them was part of the original mixed upland-herb association, or at any rate a very common part of it.

Because *Artemisia discolor* is so commonly found on erosion-pavement areas in the central part of the subalpine zone, it might be supposed at first sight to be one of the pioneers in normal succession. However, from the foregoing lines of evidence, together with the fact that Artemisia is present on few talus slopes, and on these only in places where the seed may easily have been washed in from above, it seems clear that this species has been introduced, perhaps from the adjacent lowlands where members of the *Artemisia vulgaris* complex are common.

Now consider Taraxacum briefly, in the light of its great increase shown in Table 18. This introduced weed furnishes the bulk of the forage on many sheep ranges, although it is forage of inferior volume and quality as compared with the original mixed upland-herb vegetation. The phenomenal increase in Taraxacum, both on sheep and on cattle range, is not to be explained by unpalatability, because the plant is relished by sheep and is readily eaten by cattle. Rather, the increase is to be explained by a combination of factors: a rosette growth habit, with the apical shoot meristem at or below ground level, thereby escaping direct cropping; a capacity for vigorous regrowth and flowering after being cropped; a precocious phenology and rapid maturity; and in consequence of these characteristics an enormous production of flowers and fruit.

The increase of *Helenium hoopesii*, which is poisonous to sheep, is also very marked (Table 18). Although this species is native to the Rocky Mountains, having first been collected in 1862 in "South Park and west of Pike's Peak," it was probably not abundant in the pristine subalpine vegetation of the Wasatch Plateau. At any rate it is most abundant now where the range has been denuded by severe overgrazing, and it is noted in only one of the six natural areas (Table 7). Its increase between the two surveys was less at the northern end of the plateau, where it seems to have been best established at the time of the earlier survey, than farther south, suggesting that Helenium may have been introduced at the northern end.

Permanent Plots and Quadrats

Probably the most severely abused sheep range was the crest of the plateau, along which sheep were trailed both north and south, and the eastern headwater basins and ridges. Because of persistent flooding and pollution of eastward-flowing streams, attemps were made to exclude sheep from a strip of land lying east of the crest of the plateau about the time the Manti National Forest was created, except that herds were to be permitted to traverse certain designated driveways. This strip was known variously as the "Mile Strip" and "Two-mile Strip." Grazing-use maps up through 1911 show this range to have been allotted exclusively to cattle, but there appears to have been trespass by sheep, and it is doubtful whether the boundaries of the protected strip were very consistently observed. About 1911 a deferment system was begun, by which sheep were to be held off this range until after August 20 each year. Beginning about 1920 and continuing to the present, a rotation-deferment system for sheep was adopted, one result of which has been that this range is grazed by sheep repeatedly all summer long. Although present permitted grazing is by both cattle and sheep, actual sheep grazing is much the heavier. In summary, this range has been heavily grazed for a long time, perhaps 75 years, but the grazing has at least been regulated in some measure during the latter three-fifths of that period.

On parts of the "Two-Mile Strip" many permanent meter-square quadrats and 10-meter square major plots were established between 1913 and 1919. These have been variously mapped, listed, and photographed ever since. In spite of gaps in the records, these plots and quadrats give a fairly consistent account of succession from ephemeral communities and bared surfaces to communities dominated by perennials, mostly grasses. Variations from plot to plot and quadrat to quadrat often shed significant light on the influence of site on trends.

Denuded quadrats: In 1913, five paired meter quadrats were set out in the heads of Seely Creek and Beeks Creek, and on Beeks Ridge. One of each pair was denuded by digging up the vegetation, although it appears from photographs that little topsoil, if any, was removed. The prompt reappearance of rhizomatous and bulbiferous species, as shown by subsequent quadrat charts, indicates that the subterranean parts of these species were only incompletely destroyed.

The immediate effects of denudation, as shown by the 1914 charts, were usually a decrease in perennial forbs and grasses (with the frequent exception of ruderals like *Oenothera flava, Plantago tweedyi,* and *Taraxacum officinale*), and usually, but not always, an increase in annuals, particularly *Chenopodium album.*

Comparison with the undenuded quadrats shows that recovery from denudation usually required between 4 and 10 years. Some of this recovery was probably due to resprouting of the underground parts of species not completely extirpated by grubbing. These include *Achillea lanulosa, Artemisia discolor, Aster chilensis, Delphinium nelsonii, Stellaria jamesiana,* and *Vicia americana.* But some of it was due either to current dissemination of seed, or to stored seed in the soil, of the grasses and of *Agoseris pumila, Taraxacum officinale,* and *Viola nuttallii.* Taraxacum, with its plumed fruits, gained possession of the denuded quadrats quickly, but the grasses

spread more slowly. The importance of a nearby seed source for grasses is shown by the fact that grasses were conspicuous in 1914 on those denuded quadrats which lay alongside undenuded quadrats with numerous grasses (quadrats 16, 18) but not on those lying alongside quadrats where grasses were lacking (quadrat 14) or scarce (quadrat 19).

Becks Ridge: Undenuded quadrats 13 and 15, lie about half a mile apart, each on practically level ground. The soil is essentially stable, loose and soft, with good crumb structure at the surface, and fairly high organic-matter-content—5.5% in the surface inch for quadrat 13, 6.7% for quadrat 15. Grazing by sheep is heavy.

In the first period (1913-15, Table 19), quadrat 13 lacked grasses entirely, and was dominated by Polygonum, Taraxacum, Descurainia, and Viola. "Dominated" is hardly the proper term, for a photograph made in 1913 shows that the soil surface was essentially bare. Evidently the plants were small or soon dried up, in either case providing but scanty cover.

TABLE 19. Average number of shoots per year on each of two meter-square quadrats on Becks Ridge, in three periods, 1913-48. (T17S, R4E, S23, 24. Elev. 10,000 ft.)

	QUADRAT 13, GRAZED			QUADRAT 15, GRAZED		
	'13, '14, '15	'18, '19, '23	'40, '41, '43, '48	'13, '14, '15	'19, '23	'40, '41, '43, '48
Agropyron trachycaulum	0	0	76	0	0	208
Stipa columbiana	0	0	49	0	0	1,063
S. lettermani	0	1	2,450	T	2	1,627
Trisetum spicatum	0	0	109	16	8	58
Other grasses*	0	T	1	...	...	...
Achillea lanulosa	4	2	48	823	413	160
Artemisia discolor	1	27	66	...	...	...
Erigeron ursinus	3	T	1	167	43	204
Lesquerella utahensis	...	...	...	82	86	14
Oenothera flava	14	4	0	...	...	...
Stellaria jamesiana	3	0	2	38	19	4
Taraxacum officinale	113	164	1	58	74	31
Vicia americana	27	11	54	0	0	2
Viola nuttallii	68	24	179	...	...	...
Other perennial forbs†	7	1	26	T	T	4
Chenopodium album	14	4	2	4	35	13
Collomia linearis	0	0	13	...	...	...
Descurainia richardsonii	87	18	T	...	...	...
Polygonum douglasii	626	156	137	47	356	89
Other annuals‡	3	1	1	76	10	9

*Other grasses: *Bromus carinatus* (13), *Hordeum nodosum* (13)

†Other perennial forbs: *Agoseris pumila* (13), *Delphinium nelsonii*, *Erythronium grandiflorum* (13), *Galium* sp., *Geranium richardsonii* (13), *Ranunculus inamoenus*

‡Other annuals: *Androsace septentrionalis*, *Draba* sp. (15), *Lepidium* sp., Unknown

A radical change took place between the first and third periods in assumption of dominance by grasses, mainly *Stipa lettermani,* and in reduction of annuals. This major change has resulted in adequate protection of the soil and probably improvement in its structure. It is notable that Oenothera parallels in its decline the decline of Polygonum, Chenopodium, and Descurainia, and, less clearly, that of Taraxacum. All these species thrive on bared soil, probably because competition from other plants is at a minimum. Among rhizomatous species, Achillea and Artemisia increased markedly. The increase of Artemisia recalls the general spread of this herbaceous sage (Table 18).

Quadrat 15 had a more stable cover than quadrat 13 during the first period (Table 19). The rhizomatous species, Achillea and Erigeron, were numerous and probably controlled the microenvironment. A little grass was present. Annuals were relatively scarce, although Lesquerella, a small perennial commonly found on denuded soil, was abundant. The rhizomatous dominants declined strongly in the second period, and as if "taking up the slack" Polygonum, Chenopodium, and Taraxacum increased. Other species, notably grasses, changed but little. By the third period grasses had increased enormously, and annuals had become scarce—the same essential pattern as with quadrat 13. The decline of Lesquerella from 86 to 14 plants is probably a result of its inability to flourish under taller vegetation.

TABLE 20. Number of shoots on meter-square quadrat 13, Becks Ridge, at the last four chartings, 1940-48. (T17S, R4E, S23. Elev. 10,100 ft.)

	1940	1941	1943	1948
Agropyron trachycaulum	51	152	74	25
Hordeum nodosum	0	0	0	3
Stipa columbiana	30	36	68	61
S. lettermani	957	3,097	3,610	2,138
Trisetum spicatum	60	121	98	157
Achillea lanulosa	37	36	42	79
Agoseris pumila	0	0	0	4
Artemisia discolor	135	58	36	36
Delphinium nelsonii	0	0	94	1
Erigeron ursinus	0	3	0	0
Erythronium grandiflorum	1	0	0	0
Ranunculus inamoenus	1	1	1	1
Stellaria jamesiana	0	7	0	0
Taraxacum officinale	2	1	2	0
Vicia americana	41	10	98	67
Viola nuttallii	46	36	467	168
Androsace septentrionalis	1	0	0	2
Chenopodium album	3	4	2	0
Collomia linearis	23	13	11	4
Descurainia richardsonii	0	1	0	0
Polygonum douglasii	249	158	132	9

In general, then, these quadrats show a decided improvement in vegetal cover through increase of perennials and decrease of annuals. Does this mean that the improvement is continuing? There are some indications in Table 19 that it may not be: on quadrat 13, increase of the ephemeral Viola, invasion of the annual Collomia, and persistence of Polygonum in considerable numbers in the last period; on quadrat 15, persistence of Taraxacum, Chenopodium, and Polygonum. Unfortunately, grouping four records of an 8-year span into the last period obscures whatever trends may exist. A more complete account, for quadrat 13, is given in Table 20. Here it will be seen that, although there are trends in some spe-

cies, they are neither strong nor consistent enough to indicate that the trend from preceding periods is continuing. Rather, they suggest that vegetal improvement has been at a standstill since 1940 at least. Similar lack of trend between 1940 and 1948 on quadrat 15, as well as on the denuded quadrats accompanying quadrats 13 and 15, lead to the same conclusion.

Becks Creek: There are two quadrats at the head of Becks Creek lying about one-fourth mile apart, and alongside each is another that was denuded in 1913. Undenuded quadrat 17, which is on level ground subirrigated by a small stream almost at its edge, has a harsh clay soil with low organic-matter content (2.7%). This site was probably a wet meadow before grazing by livestock began, but it has been so heavily grazed and trampled for so long that it is now fully as dry as any upland-herb site. The harshness of the soil is a result of puddling from trampling, together with the fact that there is very little vegetation or litter, because of heavy grazing, to improve the soil structure. The soil of undenuded quadrat 20 appears more severely eroded because of its rockiness (Fig. 23), but it contains more organic matter (4.0%). The slope is 19% N. 30° E. Quadrat 20, too, is heavily grazed and is probably often bedded upon by sheep. Vegetal cover of both quadrats is scantier, and surface soil poorer in quality, than cover and soil of the Becks Ridge quadrats.

Table 21 shows that quadrat 17 had a fair start in grasses in the first period, and that a material increase in grasses has occurred, but not so great as on the Becks Ridge quadrats. Here, too, annuals have declined and there has been a strong increase in the rhizomatous forbs Achillea and Aster. At the same time there are some indications that improvement is not continuing in the last period—increase in Taraxacum and maintenance of a material population of annuals. Study of the individual records, both for this quadrat and its companion quadrat which had been denuded in 1913, confirms this indication, showing that the improvement that took place between 1913 and 1940 has been halted, with no evident trend between 1940 and 1948.

Quadrat 20 and its companion denuded quadrat, on a very different site, show remarkably similar trends in vegetation, both over the entire period of record and in late years. This quadrat differs from those already described on sheep range in that accelerated soil erosion is an important environmental factor. Despite the increase in perennial vegetation, it is clear that erosion has removed an appreciable

FIG. 23. Becks Creek denuded quadrat 19 and undenuded quadrat 20, in 1913 (above) and in 1940. A virtually bare soil surface in 1913, vegetated with ephemeral species, has been replaced by a rather sparse cover of *Stipa lettermani, Achillea lanulosa,* and *Taraxacum officinale* (Table 21). Exposure of large limestone rocks in 1940 gives an indication of the seriousness of soil erosion during the 27-year interval. F-415555, F-415971

TABLE 21. Average number of shoots per year on each of the two meter-square quadrats at head of Becks Creek, in three periods, 1913-48. (T17S, R4E, S23. Elev. 10,000 ft.)

	QUADRAT 17, GRAZED			QUADRAT 20, GRAZED		
	'13, '14, '15	'17, '18, '19	'40, '41, '43, '48	'13, '14	'18, '19	'40, '41, '43, '48
Agropyron trachycaulum	0	0	8	0	2	92
Hordeum nodosum	24	24	0	...	...	...
Stipa lettermani	108	45	1,096	0	7	325
Trisetum spicatum	15	T	27	0	0	36
Other grasses*	0	2	0	...	...	...
Achillea lanulosa	54	3	172	34	4	289
Artemisia discolor	T	0	6	...	...	...
Aster chilensis	1	15	106	...	...	...
Lesquerella utahensis	0	0	4	...	...	...
Pseudocymopterus montanus	0	0	3	...	...	...
Stellaria jamesiana	26	8	21	34	30	15
Taraxacum officinale	33	4	99	4	10	215
Vicia americana	...	...	...	26	10	15
Viola nuttallii	17	11	1	34	92	15
Other perennial forbs†	18	2	32	6	10	6
Chenopodium album	0	1	0	47	4	T
Collomia linearis	83	29	72	...	...	1
Descurainia richardsonii	21	16	0	2	18	0
Polygonum douglasii	385	544	44	586	328	27
Other annuals‡	0	T	5	2	2	0

*Other grasses: *Poa* sp. (17)

†Other perennial forbs: *Agoseris pumila*, *Claytonia lanceolata*, *Crepis* sp. (17), *Delphinium nelsonii* (17), *Erythronium grandiflorum*, *Geranium richardsonii* (17), *Penstemon rydbergii* (17), *Plantago tweedyi* (17), *Solidago* (?) sp., *Viguiera multiflora* (17)

‡Other annuals: *Androsace septentrionalis* (20), *Lepidium* sp.

part of the surface soil that remained in 1913 (Fig. 23), and it is also clear from the abundant evidences of current accelerated erosion to be seen on and near the quadrat today that the present vegetal cover is too scanty to prevent continuing loss.

These quadrats show the same essential trends as those on Becks Ridge—since the beginning of record, decrease of annuals and increase of grasses, particularly *Stipa lettermani,* but since 1940 (and possibly considerably earlier) no evident trend in vegetation. Both these quadrats support materially less vegetation than the Becks Ridge quadrats, probably because of what has happened to their soils. The soil of quadrat 17, although on a site that is potentially more productive than any so far described, is puddled by the repeated trampling of sheep. The soil of quadrat 20, which originally may have been only slightly inferior to the soil of the Becks Ridge quadrats, is now greatly eroded because of loss of vegetation from excessive grazing.

Seely Flat: Quadrat 27, established in 1916, and major plot 3, established in 1915, are in a log-and-block exclosure of 12 x 12 m, on ground that is essentially level. Nearby, on similar grazed range, are quadrat 28 and major plot 6, both established in 1916. The soil in this locality, even though nearly level, is badly eroded. Organic-matter content of the surface inch is only 3.69 % (Table 4). Perceptible pedestaling of the grasses, particularly on the grazed range, shows that erosion is continuing. Notes regarding grazing use in the late fall of 1942 state: "Grazing has been severe. Many grasses have been grazed close, and all *Artemisia discolor,* except the coarsest stems, has been taken. Nevertheless, the flower heads of *Stipa lettermani* and *Agropyron trachycaulum* have largely been left."

Table 22 shows trends on the quadrats by giving average numbers of shoots in four periods. As on the other quadrats there was a marked drop in annuals after the first period. Annuals and other ephemeral species—Viola, Vicia, Stellaria, Ranunculus, Agoseris—have been dominant on these quadrats throughout, indicating a consistently low status in secondary succession. The effects of the small exclosure are apparent, through the encouragement of pocket-gopher activity, in a high population of annuals, and in a sudden drop in Stellaria after the first period. Both these symptoms were noted on similarly enclosed quadrat 23 (Table 13).

It would appear that the end of dominance by annuals and other ephemerals is now in sight. The appearance of *Artemisia discolor* in the last period is one indication. This species was present on both major plots in 1915 and 1916. It reached the quadrats by spreading vegetatively between 1936 and 1940, and in the period 1940-1948 it continued to increase on both. Its general increase in the subalpine zone has already been described from the evidence of range-survey records.

An equally striking indication of a trend toward change in dominance is provided by the increase of grasses on both quadrats. Thus this range is evidently undergoing a similar trend to that noted on Becks Ridge and Becks Creek, but is at an earlier stage in the transition. That is to say, trends that were occurring on the other quadrats 20 or more years ago are now taking place on these. The abundance of ephemerals here and the continuing increase of perennials distinguish these quadrats from most on this sheep range, where in general vegetal improvement appears to be at a standstill.

TABLE 22. Average numbers of shoots per year on each of two meter-square quadrats at the head of Seely Creek, in four periods, 1916-48. (T17S, R4E, S26. Elev. 9,900 ft.)

	QUADRAT 27, UNGRAZED				QUADRAT 28, GRAZED			
	'16, '19, '22	'24, '27, '29	'32, '34, '35, '36	'40, '41, '43, '48	'16, '19, '22	'24, '27, '29	'32, '34, '35, '36	'40, '41, '43, '48
Agropyron trachycaulum	0	45	88	121	0	0	4	135
Stipa lettermani	0	1	0	T	0	0	T	26
Other grasses*	0	6	4	64	0	T	4	28
Agoseris pumila	1	1	8	15	0	1	2	4
Artemisia discolor	0	0	0	66	0	0	0	29
Ranunculus inamoenus	3	3	11	12	1	1	0	3
Stellaria jamesiana	44	6	1	2	46	36	30	8
Vicia americana	0	2	10	76	7	10	48	30
Viola nuttallii	83	269	168	130	41	86	100	143
Other perennial forbs†	13	14	14	15	5	6	3	14
Collomia linearis	457	141	96	147	333	49	26	56
Polygonum douglasii	777	294	51	56	1,037	504	216	22
Other annuals‡	12	23	100	184	2	12	24	12

*Other grasses:
Hordeum nodosum (28)
Poa reflexa
Stipa columbiana (27)
Trisetum spicatum (27)

†Other perennial forbs:
Achillea lanulosa
Arabis lyallii
Aster chilensis (28)
Delphinium nelsonii
Erigeron ursinus
Erythronium grandiflorum (27)
Geranium richardsonii (27)
Lesquerella utahensis (28)
Oenothera flava
Pseudocymopterus montanus (27)
Taraxacum officinale
Thalictrum fendleri (27)

‡Other annuals:
Androsace septentrionalis
Chenopodium album
Descurainia richardsonii
Lepidium sp.
Orthocarpus tolmiei (28)
Small unknowns

The greater abundance of Stipa on the grazed quadrat should be noted; it will also be seen in other comparisons of ungrazed and grazed sheep range. This species had increased steadily on this quadrat throughout the period 1940-1948. It is noteworthy that Agropyron invaded the ungrazed quadrat more rapidly than the grazed quadrat, and the same is true of the respective major plots. This tendency to appear first in the exclosure is true of several other species: ***Bromus carinatus, Trisetum spicatum, Geranium richardsonii, Ligusticum porteri,*** and ***Viguiera multiflora,*** not all of which have been recorded on the quadrat. These species, while not the choicest, are preferred by sheep to many of the present dominants on the grazed range, and their increase first under protection is therefore considered significant.

Seely Slope: Quadrat 9 (and quadrat 10, denuded in 1913, which lies beside it) occupy a site that is very different from those on which other quadrats occur. It is a steep (39%) eastward slope which doubtless at one time supported a lush tall-forb community. This supposition is based upon the present partial dominance of the site by *Delphinium barbeyi* and by the persistence of a large snowbank every spring. In 1946 the ground near these quadrats became bare about July 9, five weeks later than at the Alpine plant development station. This means that the length of growing season on this site is about one-third less than that of warmer, more nearly level subalpine sites. The soil is rocky, and as the pedestaled perennials show, it has been eroding rapidly. Nevertheless it has a high organic-matter content (6.4%). The site is grazed and trailed heavily by sheep, although not so severely as years ago.

At the time that quadrat 9 was established it was dominated by rhizomatous species: Erigeron, Achillea, Penstemon, and Artemisia (Table 23). It is doubtful whether annuals ever dominated here, as they did on warmer, drier sites. Over the years rhizomatous species, except for Artemisia and Penstemon, have decreased. A very important change has been an increase in *Delphinium barbeyi,* which, because of its tall and compact growth, completely overshadows half the quadrat today. (Its true dominance is shown inadequately by a tabular comparison of numbers of shoots.) Field observation indicates that Delphinium has increased generally on this site.

Grasses have increased. The presence of *Stipa lettermani* and *Trisetum spicatum* on so moist a site is a startling anachorism. It is probably caused by the general denudation of this slope, both of vegetation and soil, which has dried it abnormally. Almost all herbaceous communities of the subalpine zone have been made abnormally dry as a result of overgrazing, but on this moist, cool site with a short growing season and with the shading effect of Delphinium, the abnormality is particularly striking.

Trends on the adjacent quadrat that was denuded in 1913 confirm those of the undenuded quadrat. Despite the strong difference in site between these quadrats and others on sheep range, the characteristic increase in grasses and persistence of certain ruderals runs true to form.

TABLE 23. Average number of shoots per year on one meter-square quadrat on slope at head of Seely Creek, in two periods between 1913 and 1948. (T17S, R4E, S26. Elev. 10,100 ft.)

	QUADRAT 9, GRAZED	
	1913, 1915, 1919	1940, 1941, 1943, 1948
Agropyron trachycaulum	0	132
Hordeum nodosum	0	22
Stipa lettermani	21	135
Trisetum spicatum	4	43
Achillea lanulosa	216	57
Artemisia discolor	9	40
Delphinium barbeyi	7	129
Erigeron ursinus	603	73
Oenothera flava	4	2
Penstemon rydbergii	13	35
Taraxacum officinale	6	38
Viola nuttallii	1	34
Other perennial forbs*	T	1
Chenopodium album	6	T
Polygonum douglasii	8	1
Other annuals†	16	0

*Other perennial forbs: *Agoseris taraxacifolia*, *Lesquerella utahensis*, *Plantago tweedyi*, *Senecio crassulus*

†Other annuals: *Collomia linearis*, *Descurainia richardsonii*, *Lepidium* sp.

The broad changes that occurred during the first 27 years of record do not appear to be continuing during the last 8: grasses are pretty much at a standstill, the rhizomatous Artemisia, Penstemon, and Erigeron have been increasing, and Delphinium has declined. The persistence of the ruderals Taraxacum and Oenothera, and a strong increase of the ephemeral Viola throughout the 8-year period, also suggest that the gains made between 1913 and 1940 are lately being lost. In this respect again, these quadrats corroborate the trends noted on others.

Little Petes Hole: Two meter-square quadrats about one-eighth mile apart were established in Little Petes Hole (S35, T17S, R4E; elev. 10,000 ft.) by A. E. Aldous in 1913. Although they were originally fenced against livestock, the fences have been down for many years, and the formerly enclosed areas are now indistinguishable from adjacent sheep range. Each quadrat slopes slightly and shows evidence of sheet erosion; however, the soil is deep and organic-matter content of the surface inch is about average —5%. This range, typical of the floors of many broad headwater basins, is heavily grazed by sheep.

Both quadrats were dominated by rhizomatous forbs, particularly Achillea, in 1913. Annuals, ephemerals (Viola, Ranunculus), and ruderals (Taraxacum, Oenothera) were rather scarce at that time. Secondary succession on these quadrats was evidently more advanced in 1913 than on the Beeks Ridge or Beeks Creek quadrats.

A photograph taken by Aldous shows that Achillea

was clearly dominant on this range in 1913. His description (Aldous 1913) of the herbaceous vegetation of the subalpine zone indicates a very different aspect than prevails today:

"The alpine zone includes the highest range on the forest. *It is nearly all open weed range,* with scattering clumps of alpine fir, and a few scattering aspens. The main weeds found in the weed type of this zone are yarrow and *Pentstemon,* with scattering bunches of larkspur at the highest elevations, with pea-vine at the lower elevations, mainly adjoining the aspen types and large patches of yellowbrush (*Chrysothamnus serrulateus*)" (emphasis supplied).

Today Little Petes Hole, and most other areas grazed by sheep in the subalpine zone, could not be classed as "weed range" because their dominant vegetation is not forbs but grass.

By 1940 rhizomatous forbs were still numerous on the quadrats, but, as on the Becks Ridge and Becks Creek quadrats, grasses had become very abundant. These were chiefly *Stipa lettermani*, Agropyron, and Trisetum. Taraxacum had increased very markedly, and Viola, Ranunculus, and Oenothera were more abundant than they had been in 1913.

Between 1940 and 1948 there is no evident vegetal trend. The persistence of large numbers of ruderals and ephemerals during this period makes it clear that the earlier improvement in perennial cover has been stopped—a conclusion that has been reached from most other quadrat records on sheep range.

Horseshoe Flat: The Horseshoe Flat quadrats (S14, T17S, R4E; elev. 10,000 ft.) are 1 x 2 m, double the usual size. One is on heavily grazed range (22E, 22W), the other is enclosed (21E, 21W). They lie on level ground which had been somewhat eroded prior to 1915 when they were established, but erosion since that time has been noticeable only on the grazed quadrat. The organic-matter content of the surface soil was determined in 1940 to be 5.2%. These quadrats represent a fairly good site, not far from the edge of a wet meadow.

At the time the Horseshoe Flat quadrats were established the dominant species was *Penstemon rydbergii*, which occurred in well-defined masses with *Achillea lanulosa*. *Viola nuttallii* was next in abundance. Some grasses were present. Over the years a more varied vegetation has developed, but of differing character on each quadrat.

On the grazed quadrat the well-defined patches of Penstemon have persisted and expanded steadily. *Stipa lettermani* has invaded and has been increasing strongly, and this grass, together with *Trisetum spicatum* and *Taraxacum officinale*, is much more abundant and persistent on the heavily grazed quadrat—as might be expected—than on the protected quadrat. The rhizomatous species, *Aster chilensis* and *Achillea lanulosa,* have also been more aggressive on the grazed quadrat.

Penstemon has increased on the protected quadrat, but much more slowly, and instead of persisting in sharply defined patches, has become broken and intermingled with taller-growing vegetation including *Viguiera multiflora, Agropyron trachycaulum, Bromus carinatus, Melica bulbosa,* and *Geranium richardsonii.* Pocket-gopher activity has been frequently noted on the enclosed quadrat, and has probably been so heavy that establishment of new plants has been handicapped. Nevertheless, the differences in succession on the two quadrats—toward dominance by xeric species under heavy grazing, and by mesic species under protection—corroborate other evidence of the influence of sheep grazing.

The fact that Taraxacum has been consistently less abundant under protection than under heavy grazing probably reflects the greater amount of foraging by pocket gophers in the exclosure as well as the competition from taller-growing species. One anomaly presents itself: *Stellaria jamesiana* is consistently more abundant on the protected quadrat despite greater pocket-gopher activity there. On other paired grazed-and-protected quadrats Stellaria is distinctly less abundant under protection, and the inference has been drawn, perhaps erroneously, that pocket gophers have reduced it by harvesting the tubers.

These quadrats have contributed a great deal toward an appreciation of the role of older vegetation in providing the microenvironment necessary for successful establishment of seedling plants (Ellison 1949a).

Current trend on the grazed quadrat is not very clear. Doubtless some improvement in cover is still going on through the slow expansion of rhizomatous species into spaces formerly occupied only by ephemerals, and through invasion by Stipa. On the other hand, the species that are increasing are either not particularly palatable to sheep (like Stipa) or are not particularly productive of forage (like Taraxacum). Furthermore, there has been a drop in Agropyron in recent years. This grazed quadrat thus supports the evidence derived from others to the effect that no very marked improvement under grazing is taking place at present.

Toms Ridge: On Toms Ridge two 10 x 10 m major plots were established in 1919, by E. V. Storm, one of which was fenced. These plots were on level ground with a deep, rich soil. At the time of establishment they were dominated by *Penstemon rydbergii* which made up roughly two-thirds of the cover. Taraxacum made up approximately one-sixth. The remaining sixth was made up of Artemisia, Achillea, Androsace, Stipa, Trisetum, and Vicia. The plots were evidently very much alike to judge from the records and from some rather poor photographs made at the time.

Gross trends on the grazed and protected plots are shown in Table 24. (The original 1919 records are different than later records in minor detail. Because they did not distinguish the proportions of grasses and other minor species, these are necessarily shown in approximations in the table.) The most marked change between 1919 and 1922 was the in-

crease in proportion of Taraxacum on the grazed range to 40%. On the protected plot Taraxacum made up about the same proportion as it had in 1919. By 1925 the proportion of grasses had increased somewhat inside the fence, but had not changed materially outside. Taraxacum was still much more abundant on the grazed range than inside the fence.

TABLE 24. Percentages of principal species on Toms Ridge grazed, G, and ungrazed, U, major plots established in 1919 and ungrazed major plot, (U), established in 1942. (T17S, R4E, S36. Elev. 10,000 ft.)

	1919		1922		1925		1942			1949		
	G	U	G	U	G	U	G	(U)	U	G	(U)	U
Grasses	8	4	2	7	4	17	39	42	5	27	19	4
Penstemon	66	66	39	51	39	45	22	12	54	15	15	50
Taraxacum	17	17	40	19	39	10	24	28	5	6	T	T
Others	9	13	19	23	18	28	15	18	36	52	66	46

The plots were not examined again until the fall of 1940. Data for 1942, however, are used here because the 1940 examination was made unduly late in the season. An additional area of open range was fenced in 1942, and a plot similar to the others was established in it.

By 1942, under continuous sheep grazing, vegetal composition had changed materially. Grasses on the grazed range had increased to about 40%, Penstemon and Taraxacum had declined. It is notable that *Stipa lettermani* made up 35 of the 39% grasses on the old grazed plot, and only 1 of the 5% grasses on the old protected plot. (The other grasses are, in order of abundance, *Trisetum spicatum, Agropyron trachycaulum, Stipa columbiana*, and, on the old protected plot only, *Bromus anomalus*.)

A second notable point is the steady increase in the proportion of "others" on the old protected plot, as compared with but slight change in this class on the old grazed plot, until in 1942 the proportion of "others" on the protected plot was more than twice as great as on the grazed plot. Species besides *Bromus anomalus* that occurred in 1942 on the protected, but not the grazed plot were:

Smilacina stellata	*Delphinium nelsonii*
Valeriana edulis	*Geranium richardsonii*
Potentilla pulcherrima	*Silene lyallii*

In 1949 the same difference in species composition was noted, with the addition of *Solidago ciliosa* inside the protected plot.

To understand the figures for 1949, two factors need to be taken into account. First, although the plots were examined at the same time of year as in 1942, the outside plot had not been grazed—probably the only examination in which this was true. In 1949, therefore, current use has not influenced the figures. Second, because of an exceptionally late spring, ephemerals (predominantly *Viola nuttallii*) which ordinarily are withered by midsummer, were still green and formed an unduly large proportion of the cover. The proportions of these were 30% on the grazed plot, 29% on the plot protected since 1942, and 9% on the older protected plot. On the grazed and recently protected plots, therefore, these ephemerals accounted for about half the "others" and for much of the apparent decrease in grasses. Making allowance for these factors, the major conclusions from the examination of 7 years before are corroborated. In addition the pattern of change noted on the older plot appears to be undergoing repetition on the plot protected since 1942: decreases in the proportions of Taraxacum and grasses.

Part of the explanation for these changes on Toms Ridge is to be found in the forage preferences of sheep. Table 16, bearing on this point, is compiled from information gathered in this same area. This shows that grasses constituted only 20% of the forage consumed, although they made up 45% of the total herbage, and that forbs in general took the brunt of grazing. Much of that which is not explainable on the basis of forage preference can be explained by phenological and morphological adaptation, particularly in the case of Taraxacum. (See p. 139.)

Upper Area B: Erosion Area B is an experimental watershed of 9 acres at the head of Ephraim Canyon. The history of grazing in Area B is given by Forsling (1931). Forsling states that Area B, between 1915 and 1929, "was grazed by sheep or cattle once or twice each summer, sufficiently heavily to prevent increase but not so heavily as to result in decreased density of the vegetation." This practice was continued until 1935. In 1935 more severe grazing was begun, continuing through 1941. Grazing was then discontinued until 1946, since when it has been extremely severe. For the most part grazing has been by sheep rather than cattle. Because the animals distribute themselves unevenly, the upper, nearly level half of the area in which this quadrat (EC4) is situated is much more severely grazed and trampled than the grazing-use statistics for the whole 9-acre area would indicate. Here the land is almost level and evidence of erosion is much less marked than it would be if the land were sloping; yet pedestaling of the grass clumps shows that material sheet wash and blowing of soil do occur.

The vegetation of this level upper portion of Area B did not change greatly between 1912 and 1924, to judge from the type maps presented by Forsling (1931, figs. 6 & 7). In both years this portion was divided between two types. The larger, with the dominants Achillea, *Stipa lettermani*, and Potentilla in 1912, had as dominants Achillea, Pseudocymopterus, and Taraxacum in 1924.

A permanent, meter-square quadrat (EC4) was established in the larger type in 1925 which shows a very marked trend in grasses up to the present (Table 25). While numbers of the principal forbs Achillea, Taraxacum, Lesquerella, and Pseudocymopterus, fluctuated without apparent trend, Agropyron declined in basal area from 289 sq cm in the first period (1925-29) to 179 sq cm in the fourth period

TABLE 25. Average basal area of grasses (sq cm) and average number of forbs per year on each of two permanent square-meter quadrats, Erosion Area B, head of Ephraim Canyon, in four periods, 1925-48. (T17S, R4E, S26. Elev. 10,100 ft.)

	QUADRAT EC3				QUADRAT EC4			
	'25, '26, '27, '28, '29	'30, '31, '32, '33, '34	'35, '36, '38, '39	'40, '41, '43, '48	'25, '26, '27, '28, '29	'30, '31, '32, '33, '34	'35, '36, '38, '39	'40, '41, '43, '48
Agropyron trachycaulum	484	381	38	26	289	413	276	179
Stipa lettermani	0	0	0	1	140	161	281	504
Hordeum nodosum	..	..	..	..	T	17	13	0
Achillea lanulosa	54	52	59	73	71	118	100	34
Artemisia discolor	4	88	225	322	T	0	0	0
Lesquerella utahensis	T	0	1	31	20	11	12	44
Penstemon rydbergii	11	11	18	30	..	..	..	..
Pseudocymopterus montanus	T	0	1	7	99	70	48	101
Taraxacum officinale	5	7	8	28	5	9	4	3
Viola nuttallii	1	1	1	5	..	..	..	..
Other perennial forbs*	4	5	3	3	2	0	0	0
Annuals†	5	2	4	6	47	6	1	2

*Other perennial forbs:
Agoseris pumila (EC3)
Oenothera flava
Polemonium foliosissimum (EC3)
Vicia americana (EC4)

†Annuals:
Androsace septentrionalis
Chenopodium album
Descurainia richardsonii (EC3)
Polygonum douglasii

(1940-48). During the same interval the basal area of Stipa increased from 140 to 504 sq cm—three and a half times.

A portion of the quadrat is presented to illustrate graphically the replacement of Agropyron by Stipa at approximately equal intervals during the period 1925-47 (Fig. 24). The development of "peninsulas," "estuaries," and "lakes" in the crowns of these grass clumps is a result of excluding in charting the dead portions which are, at least in part, associated with pedestaling of the plants by erosion.

Some factor other than grazing might be supposed responsible for these changes. For example, it is possible that some cyclic fluctuation in weather has favored Stipa over Agropyron. But there are two reasons for thinking that selective grazing, rather than weather, is responsible.

First, Agropyron is still dominant just north of the Area B fence on the same flat as the quadrat but in an area which has been ungrazed for many years. The contrast in proportions of Stipa and Agropyron on the grazed and ungrazed range is unmistakable, and as the only difference between the two areas is that imposed by the fence in keeping the animals to one side, the conclusion follows that the animals are the cause of the difference.

Second, the behavior of Agropyron on two quadrats (EC1, EC2) on nearby Erosion Area A is the opposite of that on quadrat EC4. Area A has been grazed but little since 1919, and the quadrats are not on the portions of it where animals would tend to congregate. Erosion is definitely perceptible on both quadrats, as a result of the deteriorated condition of Area A when the watershed study was begun and the fact that both quadrats are on sloping ground, but in current severity this erosion is on the order of that of the quadrat on Area B we are considering here (EC4) rather than the more rapidly eroding quadrat on Area B (EC3, described below). On both Area A quadrats Agropyron has *increased*—not declined as it should have if weather had been unfavorable.

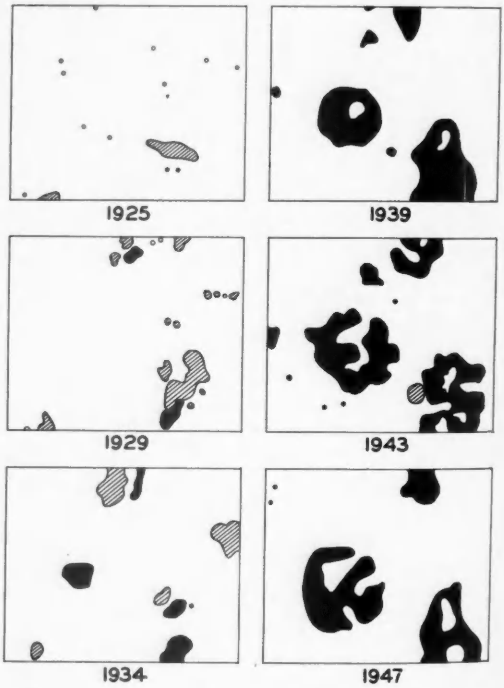

FIG. 24. A portion of quadrat EC4 showing replacement of *Agropyron trachycaulum* (hatched) by *Stipa lettermani* (solid) between 1925 and 1947. The dimensions of this portion of the quadrat are 32 x 40 cm.

Lower Area B: Quadrat EC3 in Erosion Area B was established in 1925 on sloping ground (19%) with a west exposure. The quadrat lies on a strip of soil that has been greatly eroded, with heavy erosion pavement on each side. Organic matter of the surface soil, as determined in 1935, is 4.0%. Judging by the way the animals distribute themselves on Area B, grazing had not been very heavy between 1915 and 1935 on the particular portion in which the quadrat lies. Grazing was severe in 1946 and 1947.

Table 25 summarizes the history of the quadrat in four periods. It shows that there has been a continuing decline in Agropyron irrespective of current grazing, and a continuing increase of the rhizomatous Artemisia. Other rhizomatous species, Achillea and Penstemon, have also increased. The quadrat charts show dead spaces developing in large Agropyron tufts, the breaking up of large tufts into small ones, and their eventual disappearance. In the field one can readily see that erosion is the cause, with the same pedestaling of the larger, older plants that is so common on the Wasatch Plateau. Invasion of Artemisia and increase of two other rhizomatous species (Achillea, Penstemon) undoubtedly helps check surficial erosion, but these plants make too sparse a cover to be fully effective. Nor does the increase of Lesquerella, Pseudocymopterus, Viola, and Taraxacum greatly increase effective cover. Despite these gains in vegetation, the evidence of continuing erosion is clearly visible.

The differences in history of these two quadrats illustrate the decisiveness of minor site differences in determining the trend of range deterioration. The quadrats are only a little more than a hundred yards apart, the chief difference in site being that one is on level, the other on sloping ground. On both, Agropyron has been replaced by other species. On one, erosion seems not to have been so important a factor as selective grazing, and on this quadrat the decline in Agropyron was offset by a fairly orderly replacement with the more xeric Stipa. On the other quadrat erosion has probably been a much more important factor, loss of Agropyron has been more rapid, and the only species able to colonize the unstable surface have been either rhizomatous or otherwise characteristic of xeric, eroded sites. The fact that accelerated erosion was an important factor on this slope between 1915 and 1935 when grazing was light or nonexistent is indicated by the beginning of vegetal trends that have become more evident in recent years. It would appear that, once well started on deteriorated soil, accelerated erosion may continue a long time under its own momentum.

Bear Creek: The four Bear Creek quadrats and three major plots are on the same hillside, with slopes varying from 10 to 20% and exposures from southwest to west. The soil is badly eroded and organic-matter content is extremely low, determinations in the surface inch in 1940 varying from 1.3 to 1.9%. Figure 25 shows site characteristics and gross changes in vegetation and soil over a 15-year period. Records on this hillside begin with 1916 when the original vegetation had been completely destroyed, and erosion had been so extreme that, except for scattered patches of Achillea and Sambucus, the soil surface was barren. Photographs made at the time leave no room for doubt on these points (Ellison 1943, Fig. 1a, 1949a, Fig. 1).

FIG. 25. Hillside on which part of Bear Creek quadrats and major plots are situated, in 1932 (above) and in 1947. Bunchgrasses are mostly *Agropyron trachycaulum*. A road now runs along the contour above the exclosure and this appears to have acted as a terrace, checking runoff from higher on the slope. Even so, erosion of the lower slope has been marked in this brief period, as alluvial deposits and exposure of rocks in gullies show. F-270693, F-464219

All during the period of record, vegetation has been sparse and species have been few (Table 26). Practically the only vegetation on the quadrats at the time of their establishment was Achillea. With the increases in vegetation that have occurred, cover in 1948 as measured by the point analyzer varied from 11.5 to 33% of the ground surface of the four quadrats.

Changes in vegetation on one of the Bear Creek quadrats have been described (Ellison 1943). In that analysis, however, an important factor in the increase of species invading by seed was overlooked. This was the dependence of species invading by seed on the spread of Achillea over the bare slope. Quadrat records show the spread of Achillea to have occurred between 1916 and 1929. During this period when part of each of these four separate quadrats was

TABLE 26. Average area (sq cm) of grasses and number of shoots of forbs per year on each of two meter-square quadrats at head of Bear Creek, in four periods, 1916-48. (T18S, R4E, S2. Elev. 10,000 ft.)

	QUADRAT 32, GRAZED				QUADRAT 34, GRAZED			
	'16, '18, '19	'24, '29	'32, '34, '35, '36	'40, '41, '43, '48	'16, '19	'24, '27, '29	'32, '34, '35, '36	'40, '41, '43, '48
Agropyron trachycaulum	0	3	67	61	0	3	170	402
Stipa lettermani	0	2	0	2	0	0	1	4
Achillea lanulosa	122	1,126	93	19	50	511	29	16
Pseudocymopterus montanus	4	40	56	22	0	0	1	7
Stellaria jamesiana	5	26	54	7	..	..	..	..
Taraxacum officinale	0	24	112	74	T	16	50	116
Vicia americana	..	..	..	..	0	0	5	32
Other perennial forbs*	0	1	3	T	..	..	..	..
Chenopodium album	1	0	1	T	2	27	4	T
Polygonum douglasii	T	250	4	1	4	149	4	
Other annuals†	1	0	0	0	2	2	2	T

*Other perennial forbs:
Delphinium nelsonii (32)
Lesquerella utahensis (32)
Ranunculus inamoenus (32)

†Other Annuals:
Androsace septentrionalis (34)
Descurainia richardsonii (32)
Lepidium sp. (34)
Unknown (34)

covered by Achillea and part of each was bare, there was a very marked pattern of invasion by other species. Most of the new plants became established in the area dominated by Achillea, not in the bare interspaces.

A statistical appraisal of association between seedling plants of other species and established areas of Achillea has been given elsewhere (Ellison 1949a, *pp. 100-103*), and the association has been shown beyond reasonable doubt to be real. It is illustrated in Figure 26, where dandelions and grasses are much more abundant in a patch of *Artemisia discolor* than they are on the bare ground surface.

The influence of Achillea on microclimate, in creating shade and checking wind movement, is greatest

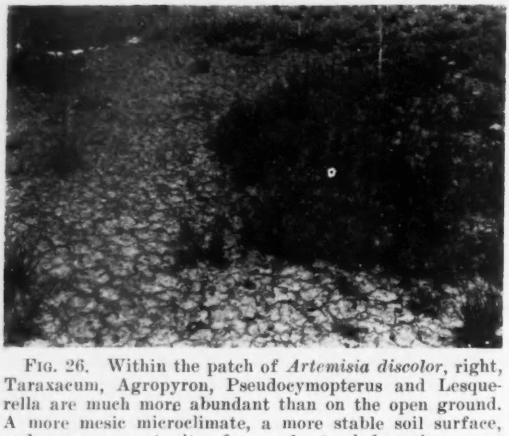

FIG. 26. Within the patch of *Artemisia discolor*, right, Taraxacum, Agropyron, Pseudocymopterus and Lesquerella are much more abundant than on the open ground. A more mesic microclimate, a more stable soil surface, and more opportunity for seeds to lodge there, encourage the establishment of seedlings within the older rhizomatous vegetation. An indication that soil fertility is not the factor that limits distribution is the vigorous growth, left, of dandelions and grasses that become established in the open. S35, T17S, R4E, 10,200 ft. elev., July 31, 1947. F-464225

when the plant is young, for only then is its growth dense and tall. As it spreads, the shoots become small and distantly spaced, and so most of the time its influence on microclimate is probably slight, although it does continue to bind the soil. Probably Achillea's contribution to soil fertility is slight, for it produces but little litter and has a rather coarse root system. The observable soil loss on this hillside during 31 years of record is certainly greatly in excess of any soil formation or amelioration that may have occurred under Achillea. The major benefit conferred by Achillea appears to have been a partial stabilization of the soil surface.

Trends indicated in Table 26 for two of the quadrats differ only in detail from those on the other Bear Creek quadrats and major plots. Achillea, the one species of consequence in the beginning, became increasingly abundant up to about 1927, and then decreased rapidly. Increases in other perennials, particularly Agropyron, Taraxacum, and Pseudocymopterus, lagged behind the increase in Achillea, but continued after Achillea declined.

With the possible exception of Vicia on quadrat 34 it is doubtful whether these species are still increasing: most of them are fluctuating without evident trend. A careful study of the data for recent years indicates a downward trend for Agropyron. Areas of Agropyron over the last 9 years of record on these quadrats are (in sq cm):

Quadrat	*1940*	*1941*	*1943*	*1948*
32	173	42	20	8
34	765	349	258	236

Sequences of quadrat charts tell the story: a seedling becomes established; the grass clump grows in diameter; dead spaces appear in the crown; the clump breaks into several smaller clumps separated by dead material; and finally even these clumps disappear.

Field observation clearly reveals the inability of this grass to get ahead of the soil erosion. Old plants of Agropyron are large and are pedestaled above the general level of erosion, often with some of their roots exposed. Commonly much of the crown is dead, and the former boundary of a vigorous tuft of grass is marked by a straggling fringe of short leaves and shoots. Some pedestals topped with dry grass stubble mark the positions of plants that have recently died. Older pedestals with no protective cover have been washed down almost to the general level, the former existence of grass revealed by a few remnants of grass roots sticking out of the soil. Successively younger, smaller, and more vigorous plants are found at successively lower erosional levels.

This erosion had been going on for years before the plots and quadrats were established, for the 1916 photographs show the surface soil to have been really a subsoil. In the history of these plots and quadrats, therefore, we have two conflicting trends occurring together: vegetation increasing at the same time that soil is rapidly washing away. Far from being uncommon, this conflict in trends is usual on sloping lands of the subalpine zone today. It is found not only on sheep range but on cattle range—almost anywhere that vegetal cover has been greatly reduced and severe soil erosion has occurred, particularly on slopes with a southerly exposure. On some slopes perennial vegetation is increasing, on some it appears to be marking time, on some, like the slopes of Bear Creek and Erosion Area B, soil loss may have gone so far that a formerly increasing trend is reversed and a loss of vegetation has begun.

Thus erosion may be so rapid and the site so seriously deteriorated that plants are unable, naturally, to gain control of the surface and completely stabilize the soil. Current grazing is a factor, no doubt, but instances are known where grazing has been light to nonexistent for 20, 30, or even 40 years, yet soil erosion continues as a ball continues rolling by momentum. During this process successive generations of plants become established, grow vigorously for awhile, are undermined by erosion, and die. In such circumstances plant succession in the ordinary, constructive sense cannot take place; the vegetation is caught in the grip of a force that cannot be overcome by the reactions of plants upon their environment. The process is not one of succession but of destruction. Such destruction, it should be added, has no analogue in normal plant succession and soil development. To speak of it as "retrogression," with the implication of going back over the same route, is to labor under a misapprehension.

Stabilization of eroding slopes like those in the head of Bear Creek is certain to be costly. Although excluding livestock may retard the rate of erosion, exclusion by itself will not do the job. This is indicated by continuing erosion on parts of Erosion Area A, the Alpine Cattle-Pasture, and the Carrying-Capacity Pasture, despite many years of protection. Artificial seeding alone is likely to be ineffective on severely eroded sites, and very intensive and costly additional measures—contour trenching and even artificial mulching—may be required. At present, however, it is impossible to prescribe a remedy, and the possibility must be faced that the soil may be so drastically deteriorated that it cannot support enough vegetation to protect itself.

LOW-SHRUB COMMUNITIES

Two low-shrub communities, one dominated by *Artemisia rothrockii*, the other by *Chrysothamnus viscidiflorus*, are conspicuous in the subalpine zone. It will be shown that both these communities, and particularly the latter, have increased far beyond their original limits, invading much of the upland-herb association during the past 50 years. For the most part, therefore, they may well be considered variants of the upland-herb association.

SAGEBRUSH COMMUNITY

The low-growing sagebrush, *Artemisia rothrockii*, occurs in large stands (Fig. 27) on Olsen Bench and Ridley Ridge (T17S, R5E, S7, 18). It also occurs northward along the top of the plateau, coming to mingle more and more with common sagebrush, *A. tridentata*, which eventually replaces it.

FIG. 27. Stand of *Artemisia rothrockii* on Swasey Ridge. Stand on distant hill is younger than that in foreground, and sagebrush is now invading grassy swale between them. Note evidence of recent accelerated erosion in foreground—shallow gully, erosion-pavement gravel, and exposed, clean-surfaced limestone rocks. S17, T17S, R5E, 10,200 ft. elev., July 2, 1946. F-443896

Site Characteristics

The site characteristics of the sagebrush community are essentially those of the upland-herb association—well-drained flats, ridges, and gentle slopes with, usually, a well-developed soil mantle essentially like that of upland-herb communities, which in most instances has been severely eroded. A soil profile, 962, on a site where it appears that relatively little erosion has occurred, is given in Fig. 28. Under the shrubs the soil is overlain with litter about 1 cm deep. The similarity between this profile and the upland-herb profiles in Fig. 9 is clear.

Even though the terrain on which the sagebrush community occurs has low erosion potential, evidence of accelerated erosion, past and present, is usually pronounced. Erosion pavement is abundant, with the shrubs hummocked above the scantily vegetated interspace level, in which exposures even of bedrock may occur.

Vegetation

Three stands on Olsen Bench, varying in the intensity of erosion they have undergone, are compared in Table 27. In each stand Artemisia makes up 75% of the vegetation present, but since the amounts of vegetation differ, absolute cover of Artemisia varies from 30% in stand 962 to 7% in stand 964.

Stand 962, with a cover (vegetation plus litter) of 78%, gives little evidence of current accelerated erosion, although the soil has been eroded to some extent in the past. Fifty-two species are listed, including many forbs palatable to sheep: Aquilegia, Castilleja, and *Erigeron speciosus* are among the most palatable. Ivesia is rare, Sedum, Actinea, and Townsendia are absent. These four latter species, together with Lesquerella and Pseudocymopterus, are common on rocky, eroded sites, and are abundant in stand 964.

PROFILE 962—ARTEMISIA ROTHROCKII
Olsen Bench, 10,000 ft. elev. T17S, R5E, S18.

Description	Sand	Silt	Clay	OM	pH	EC	EH	$CaCO_3$
Duff +1 cm. — Soil surface 0 cm.								
Reddish brown loam; granular-crumb; very friable; very many roots; no rocks. −10 cm.	26	49	25	7.4	6.4	36.8	1.8	0
Reddish brown silty clay loam; nutty to blocky with a tendency toward prismatic; rather compact; rather abundant roots, only rocks are large ones of blue limestone, carbonate-coated and forming a kind of horizon at 45-58 cm. −65 cm.	20	51	29	5.2	6.6	35.7	0.7	0
	15	50	35	4.9	6.6	38.2	0.6	0
Pale gray to tan loam as matrix around limestone rock; no structure; indurated; very few roots.	28	46	26	0.6	7.7	11.6	...	46

PROFILE 952—TALL SHRUB
Sanpete Mountain 10,500 ft. elev., T17S, R5E, S8.

Description	Sand	Silt	Clay	OM	pH	EC	EH	$CaCO_3$
Soil surface, 0 cm.								
Grayish brown clay loam; granular; friable; very many fine roots; some fragments of chert and limestone; snail shells. −25 cm.	37	34	29	9.4	7.4	48.2	...	6
	31	38	31	8.4	7.4	49.3	...	4
Grayish brown sandy loam; granular nut to weakly prismatic; fairly compact; many roots; some small limestone fragments; snail shells as deep as 87 cm. −87 cm.	59	20	21	8.0	7.5	44.6	...	6
	56	23	21	5.0	7.6	40.7	...	8
White limestone rocks in matrix of clay and some darker material from above. −107 cm.								
Bluish gray material interbedded below with whitish; few roots.	50	35	15	0.7	7.8	19.0	...	44

PROFILE 988—SPRUCE-FIR
Ephraim Canyon, 10,000 ft. elev., T17S, R4E, S27.

Description	Sand	Silt	Clay	OM	pH	EC	EH	$CaCO_3$
Duff +6 cm.								
Soil surface 0 cm.	..	..	..	40.7	6.0	75.8	11.0	0.25
Light brown clay loam; crumb; loose, friable; many roots, mostly small; no rocks. −7 cm.	..	..	..	13.8	5.9	44.9	5.4	0
Dark, faintly reddish brown silty clay; crumb; compact; many roots, large ones conspicuous; occasional limestone fragments; a little charcoal. −30 cm.	15	44	41	9.7	5.7	47.0	5.8	0
Dark brown silty clay as matrix around large limestone rocks; crumb; compact, less so than above; many roots, large ones conspicuous. −51 cm.	13	45	42	6.3	6.8	46.3	0.4	0
Olivaceous brown clay loam flecked with white and yellow as matrix around large limestone rocks; no structure; compact as in layer just above; fewer roots, but many small ones present.	31	31	38	2.8	7.4	22.2	...	41

PROFILE 999—WET MEADOW
Ephraim Canyon, 10,000 ft. elev., T17S, R4E, S27.

Description	Sand	Silt	Clay	OM	pH	EC	EH	$CaCO_3$
Soil surface 0 cm.								
Dark brown, almost black silty clay; granular; compact; very many roots; no rocks. −21 cm.	..	..	..	14.9	6.3	52.9	3.4	0
Brown silty clay; angular nut, weakly columnar in upper half; compact; many roots; scattered limestone fragments in lower half.	13	43	44	4.6	7.0	39.4	...	3
−82 cm.	13	43	44	3.6	7.2	34.9	...	6
Greenish yellow-brown or light olive silty clay; no structure; tight; no roots.	0	58	42	1.2	7.5	19.2	...	38

FIG. 28. Soil profiles under four plant communities in the subalpine zone. Analytical data are derived from samples, usually 10 cm deep, in positions shown in profile. Mechanical analysis percentages are exclusive of rock over 2 mm diam.; organic matter (OM) and lime content ($CaCO_3$) are in percent; and exchange capacity (EC) and exchangeable hydrogen (EH) are in millequivalents per 100 grams of dry soil. Horizontal solid lines indicate soil surface and division between solum and parent material; broken lines indicate minor zonal divisions and top of duff layer.

Stand 965 is intermediate in cover (53%) and character of vegetation, and shows some evidence of current erosion. Thirty-seven species are listed.

Stand 964 has only 11% vegetal cover, and has been so greatly eroded that 65% of the surface is covered by rock and gravel. This erosion pavement does much to check further erosion, but the remaining islands of soil, partly sheltered by sagebrush, are being eaten away. Most of the 38 species noted are restricted to soil remnants in the shelter of sagebrush. Exceptions are Stipa, Achillea, Crepis, Lesquerella, Pseudocymopterus, Actinea, Townsendia, and Thalictrum—except for Crepis, a hardy lot. Small trees of limber pine and Douglas-fir indicate invasion on the order of that illustrated in Fig. 42.

In general, the herbaceous understory of these stands is not distinctive and might be found on other sheep range without a sagebrush overstory. This fact ties in with the supposition that the sagebrush

TABLE 27. Vegetal composition of three stands dominated by *Artemisia rothrockii*, varying from good cover and least evidence of erosion (962) to poor cover and most evidence of erosion (964). Olsen Bench. Elev. 10,300 ft. T17S, R5E, S7, 18. Abundance symbols are explained on page 92.

Stand number	962	965	964
Vegetation, percent	40	32	9
Litter, percent	38	21	2
Bare ground, percent	22	37	24
Rock, percent	T	10	65
Grasses and sedges			
Agropyron trachycaulum	x	1	x
Bromus anomalus	x		
Carex festivella	1	1	
C. hoodii	x		
Melica bulbosa	x		
Poa fendleriana	1	1	1
P. palustris	x		
Stipa columbiana	x	x	
S. lettermani	1	2	1
Trisetum spicatum	..	x	
Perennial forbs			
Achillea lanulosa	x	1	1
Actinea acaulis	..	..	1
Agoseris pumila	x	x	
Antennaria arida	..	..	x
A. rosea	x		
Aquilegia coerulea	1	R	
Arabis lyallii	x	x	
Artemisia discolor	x	x	x
Astragalus carltonii	1	1	R
Castilleja sulphurea	x		
Clematis hirsutissima	1	R	
Crepis acuminata	R	..	x
Delphinium nelsonii	x	x	x
Erigeron eatoni	x	x	1
E. speciosus	x		
E. ursinus	x	x	
Eriogonum neglectum	x		
Erysimum elatum	x	x	x
Erythronium grandiflorum	..	x	
Frasera speciosa	x	x	R
Geranium richardsonii	x		
Helianthella uniflora	x		
Hieracium sp.	..	R	
Ivesia gordonii	R	1	1
Lathyrus lanszwertii	x		
Lesquerella utahensis	x	x	1
Ligusticum porteri	x	x	
Linum lewisii	..	..	x
Penstemon rydbergii	x		
Phacelia sericea	x	x	
Polemonium foliosissimum	x		
Potentilla pulcherrima	x		
Pseudocymopterus montanus	x	1	2
Ranunculus inamoenus	x	R	
Sedum stenopetalum	..	x	1
Senecio cymbalaroides	x		
Silene lyallii	..	..	x
Stellaria jamesiana	..	x	
Taraxacum officinale	1	1	x
Thalictrum fendleri	x	x	x
Thlaspi glaucum	x		
Townsendia montana	..	..	x
Viola nuttallii	x	x	
Zigadenus elegans	x		
Annuals			
Androsace septentrionalis	x	x	x
Chenopodium album	R		
Descurainia richardsonii	R	x	
Polygonum douglasii	R	x	
Shrubs and small trees			
Artemisia rothrockii	5	5	5
Chrysothamnus viscidiflorus	1	R	x
Pinus flexilis	..	..	R
Pseudotsuga taxifolia	..	..	R
Ribes inebrians	..	..	x
R. montigenum	x	x	x
Sambucus racemosa	x		

has invaded a herbaceous community as a result of overgrazing.

Spread of Sagebrush

The evidence that *Artemisia rothrockii* has invaded upland-herb communities as a result of denudation of cover can be summarized under three heads:

(1) *Evidence of disturbance:* Even though the sites on which *A. rothrockii* grows have low erosion potential, accelerated soil erosion is the rule. Since the current rate of erosion is incompatible with the presence of the soil mantle on which it occurs, obviously disturbance has taken place.

(2) *Age and position of bushes:* The process of invasion can be inferred at edges of the sagebrush type. In Figure 27, for example, three sagebrush stands of different character occur: one in the foreground, a younger one on the hill in the distance, and one in progress of becoming established in the grassy swale halfway between.

The bushes of the stand in the foreground have the prostrate, spreading habit of very old plants. Their hearts have rotted and the trunks have split, so that an accurate estimate of age is not possible. It appears, however, from the growth layers counted (maximum 38) and the amount of material rotted, that these bushes are at least 50 years old, perhaps older. Sagebrush occupies the site fully and the bushes look much alike. If the stand is not even-aged, the bushes are so old that minor age differences are no longer apparent.

On the distant slope a few bushes probably belong to this 50+ age class (maximum ring count 38). The majority of the older bushes are 30 to 40 years old. But there are many bushes younger than these, with a single-stemmed, erect habit. These are 20 years old or less. The stand is clearly uneven-aged, and except in spots it does not form a closed sagebrush cover.

In the swale most bushes are young. There are a very few old bushes of spreading habit and some younger bushes with ring counts of about 30. Small bushes, which are greatly in the majority, are from 10 to 13 years old.

It seems clear, therefore, that the sagebrush stands in the foreground, on the distant hill, and in the grassy swale represent at least three successive invasions.

(3) *Range-survey records:* Study of range-survey write-ups shows quite clearly that by 1936-38 the proportion of sagebrush had increased in most stands

in which it occurred in 1912-14. Moreover, sagebrush is shown to occur in many places in 1936-38 where no record of its presence was made in the earlier survey. It must therefore be concluded that sagebrush has increased. No distinction was made in either survey, however, between *Artemisia rothrockii* and *A. tridentata,* so it remains to be demonstrated that *A. rothrockii* specifically has increased.

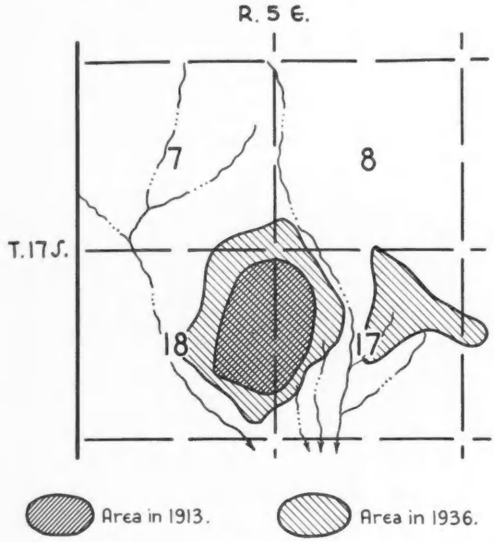

FIG. 29. Increase in area of *Artemisia rothrockii* between 1913 and 1936, as shown by range-survey maps. Each square is one square mile. Head of Olsen Canyon, elev. 10,500 ft.

Figure 29, taken from range-survey maps, shows the outline of an *Artemisia rothrockii* type on Olsen Bench in 1913 when it occupied 185 acres, and its outline in 1936 when it had expanded to an area of 376 acres. There is no confusion in this area with *A. tridentata,* for subsequent checking proves the stands in this locality to be dominated entirely by *A. rothrockii.* The principal changes in plant composition in the 23-year period are three:

(a) Increase in proportion of *Artemisia rothrockii* from 30 to 47%.

(b) Decrease in proportion of *Chrysothamnus viscidiflorus* from 25 to 15%.

(c) Appearance of *Ivesia gordonii,* not mentioned in 1913 but estimated in 1936 to make up 4% of the cover.

A second type of 105 acres was outlined on Swasey Ridge in 1936 which had not been noted in 1913—despite the fact that the 1913 surveyor's traverse led across this particular area. It is also known, from ring counts described under (2) above, that bushes of *A. rothrockii* were growing on at least part of this area in 1913. Thus it is probable that in 1913 the stand was either too small to be mapped or had not yet become sufficiently distinct, through thickening of sagebrush, to be separable from the large "3-yellowbrush-grass" type that was made to include it. Sagebrush was not included in the description of the large type, so it was probably not very abundant in 1913.

At this point a hypothesis may be presented to account for the sharp break in boundary so often seen between the sagebrush community and adjacent grassland. Examination of soil profiles has failed to show any evidence that the sharp change is caused by soil differences; indeed, the similarities between the soils of the two types are more remarkable than the differences. The facts that stands of *Artemisia rothrockii* occur on eroded soils, that they have spread in recent times, and that they are still slowly spreading, suggest that the type boundaries in many cases may correspond with the boundaries of areas that were most severely denuded of herbaceous cover during the early days of most abusive grazing. Such areas would provide the least impediment to invasion by sagebrush; furthermore, their continuing erosion suggests that they may at one time have been stripped of most of their vegetation.

No one knows what the fate of the sagebrush community would be under proper grazing and with accelerated erosion no longer a factor. No instances are known where these conditions have existed long enough to suggest an answer. Under extreme accelerated erosion, on the other hand, like that prevailing in stand 964 (Table 27), the sagebrush itself is destroyed and the erosion-pavement community replaces it. In stand 964 at the present time there is only about one-fourth of the sagebrush cover that exists in stands 962 and 965, and erosion-pavement forbs are prominent.

Before leaving the sagebrush community further mention should be made of the common sagebrush, *Artemisia tridentata.* From inspection one is led to conclude that this shrub is invading the uplands at the northern end of the plateau, and the observation is confirmed by evidence from permanent plots on Gentry Mountain and the head of Cove Creek, where sagebrush has invaded lately.

Taking into account field observation, the range-survey records involving *A. tridentata* (as opposed to those involving *A. rothrockii*), and the evidence from these plots, there can be no doubt but that this lowland sagebrush, a characteristic species of the valleys and foothills, has spread in the subalpine zone. Its spread provides one more indication (as the spread of *A. rothrockii* and of *Chrysothamnus viscidiflorus* probably do also) of induced xeric conditions in the normally mesic environment of the subalpine zone.

YELLOWBRUSH COMMUNITY

The yellowbrush community dominated by *Chrysothamnus viscidiflorus,* is widely distributed in the subalpine zone of the Wasatch Plateau, much more widely than the sagebrush community. An even greater volume of evidence indicates that Chryso-

thamnus has recently invaded areas formerly dominated by herbaceous vegetation, evidently as a result of overgrazing's having thinned the original cover and induced erosion.

Chrysothamnus viscidiflorus is most abundant east of the crest of the plateau. Relatively little occurs on the steeper western face. It is by no means restricted to the subalpine zone, but occurs in abundance in eastward drainages into Joes Valley and Scad Valley (T15, 16S, R6E), and on the eastern outliers of the plateau.

Site Characteristics

Chrysothamnus grows best in the open; it never occurs under coniferous forest and occurs uncommonly as an understory to aspen. It obviously requires warm, dry sites, and in the subalpine zone grows most commonly on level ridges, flats, and very gentle slopes, usually with a sunny exposure. There are no stands in any of the small natural areas that have been found. On Elk Knoll a few plants occur on a warm, dry, southwest-facing slope which has been eroded. An old sagebrush (*Artemisia tridentata*) also grows here at 10,000 ft., clearly out of place, which leads one to suspect that both are invaders from the lowlands, perhaps introduced 50 years ago when Elk Knoll was grazed by sheep.

The boundary between yellowbrush and herbaceous communities is usually sharp. This fact suggests that inherent differences in soil may account for the boundary; but a number of paired profiles dug in yellowbrush stands and in nearby grassland have failed to show material or consistent differences.

It is notable, however, that the soil in yellowbrush stands often shows evidence of severe erosion. Such stands may be found on rocky knolls or on shallow soil at the edges of terraces; but sometimes they occur, with the evidence of past erosion, on extensive level areas (Fig. 30). The spread of Chrysothamnus revealed by comparison between range surveys made in 1912-14 and 1936-38 has often been from areas of more rapid to areas of less rapid erosion. It is also notable that the only evidence of current invasion of grassland by Chrysothamnus is in areas that are severely grazed so that considerable bare soil is exposed—although the seedling plants are found in grass tufts rather than on the bare ground (Ellison 1949a, *Fig. 5*). In short, since these observations suggest that the occurrence of Chrysothamnus is related to soil erosion, one is led to suspect that it originally became established on areas where the herbaceous cover had been thinned or destroyed by overgrazing. A similar explanation has been given to account for stands of *Artemisia rothrockii.*

On gently rolling terrain, like much of Horseshoe Flat, yellowbrush is concentrated on slightly elevated sites. Lower-lying sites are usually dominated by *Stipa lettermani,* sometimes by *Penstemon rydbergii* and *Artemisia discolor.* Differences in local climate and soil seem too slight to account for this sharp alternation between shrub- and herb-dominated

FIG. 30. Stand of Chrysothamnus in 1917 (above) and in 1941, showing thickened cover on heavily grazed sheep range. Note development of erosion pavement by 1917. Close observation reveals evidence of active erosion today, despite more effective soil protection. Aspen in background is dying out because of sunscald and because root sprouts are annually browsed off to the ground by sheep. Wagon Road Ridge, 9,700 ft. elev.
F-415451, F-416100

communities. The puzzling pattern is probably explained by grazing. Horseshoe Flat was once grazed by bands of sheep that were held in one locality all summer long. This practice was vividly described to me by James Jensen of Spring City, who herded sheep on Horseshoe Flat as a boy around 1880. The sheep, as sheep will, unquestionably bedded on the most elevated sites night after night, denuding the soil there more completely than elsewhere. These denuded spots would then have provided the best place for invasion and increase of yellowbrush. Its present occurrence on low rises thus probably conforms to a former pattern of grazing intensity.

After it becomes established, the yellowbrush community may provide enough cover to protect the soil very well. About 1919 on Poison Ridge (T11S, R5E, S26), for example, Chrysothamnus invaded on a surface that had been virtually denuded, as photographs show, and was eroding to the point where a definite erosion pavement developed, which is visible even yet. Today the cover is so dense, between

Chrysothamnus crowns and Stipa in the interspaces, that the soil appears to be safely stabilized. As another example, photographs made in 1917 on Wagon Road Ridge (T18S, R5E, S10) show heavily grazed yellowbrush stands with erosion pavement conspicuous between the bushes. At present the interspaces are occupied by Stipa to such an extent that certainly less erosion is now taking place than in 1917 (Fig. 30).

Vegetation

The following description of a yellowbrush stand on Poison Ridge gives an idea of the characteristics of the community. This particular range is grazed by sheep, but much less now than formerly. In 1919 it was virtually denuded. Now the cover of brush and grass is adequate to protect the soil. The most common species, with the symbols of relative abundance used in other tabulations, are:

Chrysothamnus viscidiflorus	4
Stipa lettermani	3
Achillea lanulosa	2
Agropyron trachycaulum	2
Symphoricarpos oreophilus	1
Viola nuttallii	1
Bromus carinatus	1
Orthocarpus tolmiei	1
Phacelia heterophylla	1
Rudbeckia occidentalis	1
Vicia americana	1

Less abundant species are:

Artemisia tridentata	*Melica bulbosa*
Agoseris pumila	*Penstemon (cyananthus?)*
Chenopodium album	*Poa pratensis*
Collomia linearis	*Polemonium foliosissimum*
Crepis acuminata	*Polygonum douglasii*
Delphinium nelsonii	*Stellaria jamesiana*
Descurainia richardsonii	*Taraxacum officinale*
Erysimum elatum	*Thalictrum fendleri*
Geranium richardsonii	*Viguiera multiflora*
Lupinus alpestris	

On this particular range dead stubs and severely hedged bushes of Symphoricarpos are found, indicating that this bush was formerly more abundant. In an exclosure fenced against sheep since 1919 Symphoricarpos has reasserted itself. Penstemon, Geranium, and Viguiera have also become more abundant where protected from sheep.

The oldest quadrat record showing positions of individual plants goes back to 1913. The quadrat (on Wagon Road Ridge, T18S, R5E, S9) was fenced when it was established. Figure 31 shows the positions of bushes on the quadrat in 1913 and 1943. Only basal area is shown in 1943; crownspread practically covered the entire quadrat. Several new bushes appeared between the first mapping in 1913 and the second mapping in 1940. The facts significant to the present discussion are the evident persistence of nearly all the 1913 plants to 1943, and subsequent chartings which show no material change to 1948. It is a matter of record, therefore, that individual bushes have lived at least 35 years.

Ascertaining the age of Chrysothamnus by count-

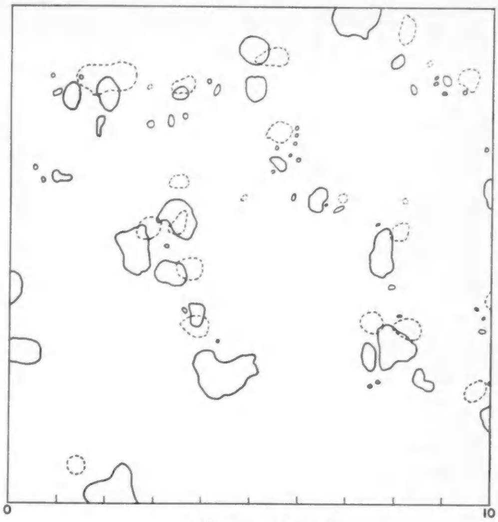

FIG. 31. Chrysothamnus on meter-square quadrat M-2 in 1913 (broken lines) when the plot was first fenced against livestock, and in 1943 (solid lines) after 30 years' protection. Outlines in 1913 are probably total crownspread of severely hedged plants. Outlines in 1943 represent basal area only, crownspread being so great as almost to cover quadrat.

ing growth rings is not difficult with plants up to about 35 years of age. In old plants heartwood becomes rotten and stems break apart, so that estimates are liable to error. It is of course possible to estimate the age of old plants by correlating diameter with age in sound-stemmed plants and applying this relation to the diameter of rotten heartwood. This was done in 1944 in the course of cutting off 456 Chrysothamnus bushes in a transect 1 m wide and 55 m long through part of a stand on the ridge separating Seely and Ephraim Creeks (S26, T17S, R4E). This ridge has been used as a driveway since this range was first grazed by sheep. Most of the surrounding area is now covered with erosion pavement which, with evidences of accelerated erosion in soil remnants, reflects the severity of grazing and trampling the ridge has suffered.

The oldest bushes that could be dated with reasonable certainty appeared about 1885, suggesting that Chrysothamus lives at least 60 years. Numbers of bushes increased in each succeeding 5-year age class, the younger bushes tending to fill in between older ones more rapidly than they advanced into the larger grassy openings, although they were advancing. This tendency for the stand to thicken may be assisted by reduction in herbaceous competition through trailing and grazing in the spaces between older bushes.

Dating the oldest bushes in the 1880's has further significance on the edge of this old driveway because it relates the establishment of Chrysothamnus here

to the beginning of intensive overgrazing and soil denudation. The continuing increase of Chrysothamnus on the area is obviously related to this continuing cause.

Trends on Grazed and Protected Range

On heavily grazed sheep range Chrysothamnus tends to be stunted because it is browsed back in the fall. On range grazed only by cattle, which browse it little if at all, *Chrysothamnus* grows relatively tall. As with *Artemisia rothrockii,* plants associated with Chrysothamnus are those of the drier upland-herb communities. On heavily grazed sheep range, forbs and the more palatable grasses, *Poa fendleriana* and *Agropyron trachycaulum*, tend to be restricted to the shelter of bushes, while less palatable and more xeric species, particularly *Stipa lettermani,* occupy the interspaces.

The following comparison, made in 1942, contrasts typical yellowbrush vegetation on grazed range with that inside a small exclosure built by Mark Anderson in 1914 (T12S, R5E, S25):

1. Chrysothamnus is larger inside the exclosure than on grazed range. The bushes are taller and their crowns make an almost continuous cover. On comparable grazed range the bushes are widely spaced.

2. *Stipa lettermani* is very abundant outside in the spaces between shrubs; scarce inside. It occurs inside the exclosure largely on spots which look as if they have been gopher mounds at some time during the past several years.

3. *Agropyron trachycaulum* is abundant inside the exclosure, scarce outside. Most of the plants that occur outside are sheltered by bushes; inside they occur between bushes as well. The heavy-headed plants inside, reaching a height of almost 70 cm, contrast sharply with plants that reach only about 45 cm outside. Although wheatgrass overtops yellowbrush, there is no indication that yellowbrush is declining. (This observation is equally true of stands of Chrysothamnus that have been lightly grazed in recent years.) If yellowbrush gives way to forbs and grasses, the process takes longer than 28 years.

4. *Bromus carinatus* occurs inside the exclosure; none is found outside.

5. Old *Artemisia tridentata* bushes are about as abundant inside the exclosure as outside, but there appear to be fewer young bushes inside. Numerous seedlings of the current year (1942) occur both inside and outside.

Another exclosure, established in 1913 on Wagon Road Ridge (T18S, R5E, S9) by A. E. Aldous tells essentially the same story. Here bushes on the grazed range average 23 cm in height, while those in the exclosure average 35 cm. The difference in bush crownspread is even more marked. In 1940 two sample plots, each 2.5 x 4 m, were laid out, one within the exclosure and one on comparable, adjacent grazed range, upon which plants were counted. Numbers of plants were as follows:

	Grazed	*Protected*
Chrysothamnus viscidiflorus	143	225
Agropyron trachycaulum	38	45
Stipa columbiana	6	6
S. lettermani	333	119
Festuca ovina	45	7

The differences in Agropyron and *Stipa lettermani* are somewhat less marked in this comparison, but parallel those in the comparison just made. Abundance of Festuca is undoubtedly correlated with the bare soil surface and development of an erosion pavement on the grazed range. The soil of the fenced plot, in contrast, is covered with a layer of litter 1 to 2 cm deep.

In 1913, when the exclosure was built, a permanent meter-square quadrat was established inside it, from which Figure 31 has been derived. Numbers of shoots of the various forbs and grasses in 1913, as compared with the average since 1940 are:

	1913	*1940, '41 '43, '48*
Stipa lettermani	1,200	1,394
Agropyron trachycaulum	—	469
Other grasses	44	10
Lathyrus lanszwertii	155	23
Taraxacum officinale	3	34
Other forbs	—	4

In total numbers Stipa has changed little, but Agropyron has increased from nothing (or from very little, if in 1913 some Agropyron was mistakenly included among the minor species here grouped as "other grasses"), until now it is codominant with Stipa among herbaceous species. The basal area of Agropyron is approximately equal to that of Stipa. The decline in Lathyrus may or may not be significant—there are too few other plots containing this species to support either conclusion. The increase in Taraxacum, paralleling similar increases in other parts of the subalpine zone, probably reflects the very great seed source that exists on the adjacent grazed range.

A pair of 100 sq m permanent plots established on Poison Ridge in 1919 (T11S, R5E, S26) demonstrate invasion by Chrysothamnus. Individual bushes were not mapped in 1919. Photographs of the two plots and descriptions of vegetal composition indicate that but little Chrysothamnus was present at that time. The establishment report by Earl V. Storm states:

"The vigor of all plants is good; porcupine grass is exceptionally strong with indication of a good seed crop production. The predominance and vigor of this grass on adjacent range associated with yellowbrush, may signify that within a short time these two plants will take the area."

Storm's prediction came true. By 1925, the date of next examination, *Chrysothamnus* bushes were as much as 15 in. tall and 24 in. in diameter. On the fenced plot 22 plants were recorded and on the grazed plot 55. By 1942 the numbers of bushes in three size classes were as follows:

CROWNSPREAD	*Fenced Plot*	*Grazed Plot*
One-fourth sq m or more	13	28
One-tenth to one-fourth sq m	147	74
Less than one-tenth sq m	748	1,136
Total	908	1,238

From this plot as well as from other evidence it is clear that one of the characteristics of Chrysothamnus invasion under grazing is "consolidation of position" through continued thickening of the stand.

Invasion of upland-herb vegetation by Chrysothamnus in the subalpine zone is clearly demonstrated in comparing records of the 1912-14 and 1936-38 range surveys. Of 224 land-survey sections on which this species was reported, 169 showed a definite increase in area covered by Chrysothamnus, 12 a definite decrease, and 43 little change (Table 18). In terms of percentage composition the increase was somewhat less marked (increase 153, decrease 43, little change 28); but bearing in mind that other species have generally increased since 1913, which tends to diminish the proportion of Chrysothamnus, it must be concluded that this relative increase in proportion is also probably real.

Figure 32 illustrates increase of area on a block of eight mile-square sections. Positions of the four areas of Chrysothamnus in 1913 are roughly in agreement with the areas independently mapped in 1937. The shifting northward of the type boundaries in sections 29, 30, and 32, which correspond with edges of the ridge, represents errors in mapping in unsurveyed terrain. In these eight sections the total area of types containing Chrysothamnus in 1913 was 2,210 acres, and in 1937, 3,430 acres, an increase of 55%.

It may appear paradoxical that a species so heavily grazed by sheep as Chrysothamnus should have spread so greatly on sheep range. Reference has already been made to the stuntedness of bushes browsed by sheep; that they can survive browsing of the severity that many receive is indeed surprising. However, sheep often do not graze Chrysothamnus until fall, and not always heavily every fall. Perhaps the bushes suffer less damage during this limited fall period than they would if they were subject to season-long grazing of the same intensity. Usually most have flowered and many have fruited by the time they are grazed. And finally, the fact has been pointed out that young Chrysothamnus plants tend to occur abundantly in tufts of *Stipa lettermani.* This grass is one that has been shown to have increased consistently on sheep range. Being little grazed by sheep when mature, Stipa provides a measure of protection while yellowbrush seedlings are becoming established. These several factors combined may explain why yellowbrush has increased in the face of heavy grazing.

COMMUNITIES OF EPHEMERAL SPECIES

POLYGONUM-VIOLA-STELLARIA COMMUNITY

This community is characterized by species of three different growth forms having in common the characteristic of withering by midsummer during most years. The name "ephemeral" refers to this characteristic.

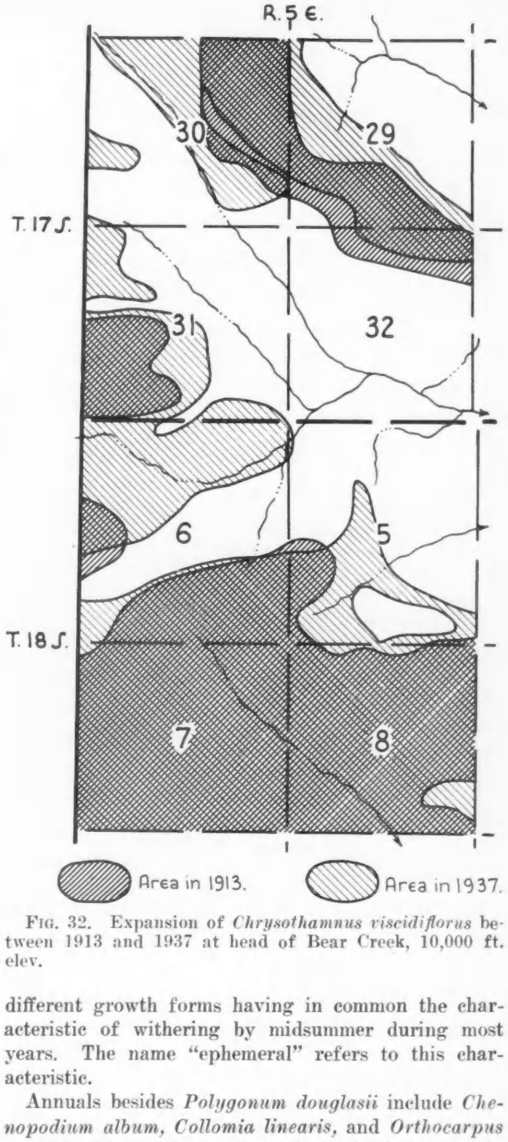

FIG. 32. Expansion of *Chrysothamnus viscidiflorus* between 1913 and 1937 at head of Bear Creek, 10,000 ft. elev.

Annuals besides *Polygonum douglasii* include *Chenopodium album, Collomia linearis,* and *Orthocarpus tolmiei. Madia glomerata* tends to dominate certain stands so distinctively that these stands are given separate recognition. Perhaps *Descurainia incisa* and *Androsace septentrionalis,* which occur in the subalpine zone as biennials, should be grouped with these annuals. Sampson (1919) considered these species and a few other annuals to make up the "ruderal-early-weed consociation" or "first-weed stage" in succession.

The second growth form includes taprooted perennials of a ruderal or semiruderal nature. Of these, *Viola nuttallii* is most abundant. *Taraxacum officinale* and *Oenothera flava* are somewhat less ephemeral, but sufficiently similar to be grouped with it. Sampson

considered these three species among those characteristic of the "early second-weed stage."

The third growth form includes tuberous or bulbous species with weak stems: ***Stellaria jamesiana, Vicia americana,*** and the vernal species ***Delphinium nelsonii, Orogenia linearifolia, Erythronium grandiflorum,*** and ***Claytonia lanceolata.*** All these species are also legitimate members of communities higher in secondary succession.

These ephemeral species, particularly the annuals, are characteristically abundant on disturbed soils. Areas that are plowed for seeding of perennial species, particularly when the seeding fails, are covered by a dense growth of Chenopodium, Descurainia, and Polygonum. Usually the annuals are not so abundant the first summer as later, but they are large, and by the second summer they occur in enormous numbers.

Several decades of overgrazing destroyed perennial plants years ago, and intensive trampling disturbed the soil thoroughly. Ephemerals were then dominant over very large areas. At present there is materially less congestion and trailing in handling livestock than formerly, and dominance by ephemerals is correspondingly less.

Characteristically the Polygonum-Viola-Stellaria community is found on flats and gentle slopes. Its occurrence is conditioned by gentle topography: an erosion potential so low that some soil has been retained (more rapidly eroding soils have deteriorated to erosion pavement or bedrock), and a terrain subject to disturbance by animals. Livestock tend to concentrate on flats, and the workings of pocket gophers appear to be more abundant on flats than on steep slopes.

Soil

The soil that supports this community is not necessarily deteriorated, but in point of fact practically all soils that support it today are deteriorated as a result of inadequate vegetal protection and consequently long-continued erosion. Using field peas and wheat as phytometers, Sampson (1919) demonstrated that productivity of "ruderal-weed soil" was lower and water requirement higher than of "wheatgrass soil." In later tests additions of ammonium sulphate and treble superphosphate have increased yields of ***Bromus carinatus*** an average of 46%. (Data in files of Artificial Revegetation Project, Intermountain Forest and Range Experiment Station).

Repeated analyses have demonstrated that soil under ephemeral vegetation contains less organic matter, nitrogen, and phosphorus than soil supporting permanent perennial cover. Sampson (1919, *p. 49*), and Stewart & Forsling (1931) present some data on the chemical deficiencies of this soil. An example of its deficiency in organic matter is contained in analyses of samples obtained in bare spaces sparsely vegetated with ephemerals as compared with nearby patches of ***Penstemon rydbergii*** where the surface was sheltered by dense vegetation (Ellison 1949a, *Table 8*). This showed that soil under ephemeral vegetation was poorer in organic matter than soil under persistent vegetation, and that the surface centimeter contained little, if any, more organic matter than the 3-15 cm level. Ephemerals, in other words, do not create an organic-matter gradient like that in soil under an erosion-resistant, perennial cover.

But pot cultures and chemical tests do not give a definitive answer to the question as to why perennial vegetation is so scanty on this soil. Productivity, or luxuriance of growth, is one thing; plant establishment is something else. A demonstration that a plant grows less luxuriantly on one soil than on another is not proof that it cannot grow on both.

There is ample evidence to show that perennial species can grow on this denuded soil. They grow luxuriantly in pot cultures where the soil is kept well supplied with water, indicating that the water relations of this eroded clay are more likely than its chemical content to hinder establishment. Perennials have been successfully seeded artificially and, as observation and permanent plot records show, they have, in time, invaded naturally. There is little likelihood that ephemeral vegetation adds materially to the fertility or physical improvement of these soils. It provides such inadequate cover that losses from accelerated erosion in all probability more than cancel out whatever contributions the scanty vegetation may make to fertility or tilth. Hence natural invasion of perennials cannot reasonably be attributed to improvement of the soil by ephemeral vegetation.

Many factors operate to check invasion of more persistent species into ephemeral vegetation. Lack of seed may be a factor in some places. Competition from ephmerals is certainly a factor in some. An adverse microclimate, which is correlated with adverse soil structure and rapid surface drying, is another factor, or factor-complex. Low infiltration is a related factor. Selective grazing of the invading perennials is another factor. Repeated disturbance of the surface by pocket gophers is still another. In my opinion, any one of these various factors is more likely to be limiting than low fertility. Taking them all together, and including low fertility, they provide a reasonable explanation for the apparent inability or slowness of more persistent species to replace ephemerals.

Vegetation

The Becks Ridge and Becks Creek quadrats, when established in 1913, provide a description of this vegetation (Tables 19, 21, Fig. 23). Considering Becks Creek quadrat 20 in 1913 alone, a total of 422 plants was recorded. Over half (274) were Polygonum. In descending order were: Chenopodium (46), Viola (32), Stellaria (31), Vicia (27), Achillea (11), and Erythronium (1).

Other descriptions are variations on the same theme, some with more rhizomatous perennials like Achillea and *Erigeron ursinus,* others with more taprooted perennials like Viola and Taraxacum. Much of the

variation depends on the time of year the vegetation is observed. Orogenia, Erythronium, Delphinium, and Claytonia wither particularly early, and for that reason are recorded only erratically on quadrat charts.

Ephemeral communities are less widespread today in a pure form than they were 30 or more years ago. There are at least two reasons for this change. One is that, in many places the ephemerals have been succeeded by more persistent species, as the quadrat records have shown. Even in stands still dominated by annuals, there are usually many perennial plants (Fig. 33). This change undoubtedly reflects improvements in livestock management to reduce trailing and trampling. The second reason is that certain soils which once supported annuals in dense stands have been so greatly eroded that now they support little vegetation of any sort.

FIG. 33. An ephemeral community on an eroding slope in which perennials are invading, August 19, 1943 (above) and August 29, 1948. Although grasses (*Bromus carinatus, Agropyron trachycaulum,* and *Stipa lettermani*) increased considerably in the 5-year interval, this was mostly in the drainageways. Pedestaling on the open slopes makes it doubtful whether grasses can increase fast enough to hold their ground. Note spread of rhizomatous *Artemisia discolor* in foreground at left. Head of Bear Creek, S35, T17S, R4E, 10,000 ft. elev. F-426999, F-464245

It is notable, too, that some weed species are scarcer in these stands than formerly. *Chenopodium album, Lepidium densiflorum,* and *Monolepis nuttalliana* are seldom encountered today, but they appear to have been fairly abundant, particularly on bedgrounds and in corrals, years ago.

Succession

The successional relations of ephemerals are very clear and well defined. Their dominance is accompanied by soil erosion and in time, when subsoil alone is left, loss of nearly all vegetation. If bedrock is exposed, certain plants will grow in the crevices. If erosion pavement is formed, a characteristic community of plants, similar to the early stage in primary succession on young soil developing from limestone talus, will be found. The process of soil destruction is so common that there can be no question of the reality of this alternative.

Secondary succession toward perennial vegetation is also easily observed (Fig. 34). Relative ages of patches of *Penstemon rydbergii, Artemisia discolor,* and *Achillea lanulosa* can be told by the areal spread, compactness, and height of the patches (Fig 18).

FIG. 34. An ephemeral community on the flat, dominated by *Viola nuttallii, Polygonum douglasii,* and *Stellaria jamesiana,* being invaded by *Artemisia discolor* (light gray circular patches) and *Penstemon rydbergii.* The square outline of shrubs (*Sambucus racemosa, Ribes montigenum*), about 100 ft. on a side, marks the position of a former log fence. Head of Jimmies Fork, Ephraim Canyon, 9,900 ft. elev. August 3, 1945. F-443848

The process of invasion of these species, included in Sampson's (1919) "second-weed stage," into an ephemeral community is therefore easy to infer. It is also easy to infer invasion by bunchgrasses like *Agropyron trachycaulum* and *Bromus carinatus,* or by forbs like *Geranium richardsonii* and *Erigeron speciosus,* in which size and age class can be related (Fig. 20). Permanent meter quadrats and larger plots have given a more accurate measure of invasion and confirm the inferences drawn from inspection.

The invasion of Sambucus and Ribes into an ephemeral community following the line of an old corral fence is illustrated in Figure 34. A few of the original notched logs from which this corral was built, probably 50 or more years ago, are still lying on the ground. This phenomenon, less clearly marked, is to be seen along more recent fences. But the invasion of Sambucus is not restricted to fence lines. This species is known to have invaded depleted range

from the evidence of old photographs, and it has increased on at least one major plot (MA-1) since 1914, in a tarweed stand. *Rudbeckia occidentalis* also has increased greatly on this tarweed plot.

In short, subsequent observation supports the essential validity of Sampson's conclusion that the ephemeral community is lowest in the scale of succession—if this be understood as secondary succession, where a soil mantle, intact or eroded, persists.

TARWEED COMMUNITY

A community dominated by the annual tarweed, *Madia glomerata*, is treated separately from the Polygonum-Viola-Stellaria community because of its distinctive dominant. Madia invades denuded areas on the same types of soil and topography as other annuals, and like other annuals, it usually makes a scanty vegetal cover. Unlike many annual weeds, however, Madia seldom occurs directly under an aspen canopy and seldom occurs as a minor component of perennial vegetation. Where it occurs it is usually either dominant or codominant with other ephemerals. While in the same relative position successionally as other communities of ephemerals, that is, at the bottom of the secondary successional ladder, the tarweed phase evidently supersedes and dominates the others under continued heavy grazing wherever Madia has been introduced.

Table 28, showing vegetal composition of two quadrats, gives an idea of the persistence of the community under heavy grazing. Here grasses have increased since 1914, although most of the plants are small. Charting in 1948 was done about a month later than in the other two years, and this accounts for the apparent disappearance of Viola, Stellaria, and some annuals. The chief fact brought out by this table is the dominance of the site by Madia for at least 34 years.

TABLE 28. Average number of shoots/sq m on two permanent meter-square quadrats (62, 63) in Madia community: 1914, 1942, and 1948 (S7, T12S, R6E. Elev. 8,600 ft.)

	1914	1942	1948
Agropyron trachycaulum }	7	144	36
Bromus carinatus } ...		164	232
Lathyrus lanszwertii........	8	7	13
Rudbeckia occidentalis.......	2	...	...
Stellaria jamesiana.........	24	178	...
Viola nuttallii.............	29	32	...
Androsace septentrionalis....	2	...	...
Chenopodium album........	30	30	1
Collinsia sp...............	29	...	...
Collomia linearis..........	39	54	1
Descurainia richardsonii....	T	...	...
Galium sp................	24	13	...
Gayophytum ramosissimum..	6	...	...
Madia glomerata..........	556	1,816	824
Polygonum douglasii........	312	290	302
Symphoricarpos oreophilus...	T	...	...

Spread of Madia

A comparison of range-survey data made in 1913-14 and 1936-38 shows that Madia has spread greatly on the plateau during this 23-25 year interval, and the data provide clues as to where it came from and how it spread. Madia is so distinctive, because of its tendency to dominate annual stands and because of its strong smell, that range-survey comparisons involving it are believed to be particularly reliable.

Townships 10 to 13S, at the extreme northern end of the main axis of the plateau, were examined when the survey was beginning and methods were being developed in 1912. These records cannot be used in this comparison because Madia cannot be distinguished with certainty, although it was probably abundant in these townships in 1912. One reason for thinking so is that Madia was collected for identification in a "sage area in Gooseberry Valley" (T13S, R6E) August 8, 1912. The collector noted that the plant was very common on the Manti Forest and seemed to invade as a result of overgrazing. Inasmuch as the range-survey crew had been working in townships 10S to 13S prior to this collection, and were working in township 13S at the time of collection, this note suggests that Madia was common in these townships. Furthermore, in T12S, R6E two years later, it was dominant on two permanent meter quadrats (Table 28).

Townships 14 and 15S, where Madia is now abundant on the main axis of the plateau, were examined in 1914, but no Madia was reported at that time. Its absence in 1914 must be considered real rather than an error, for Madia had been reported elsewhere on the plateau both in 1913 and in 1914.

That Madia has spread southward along the main axis of the plateau above Fairview, Mount Pleasant, and Spring City is indicated by the later range survey alone. It happens that the crest of the plateau roughly coincides here for more than 11 miles, with the north-south township line between ranges 5E and 6E. Considering the land-survey sections lying 2 mi. east and 2 mi. west of this line—that is, a strip 4 mi. wide and 11 mi. long—and breaking this strip into 11 tiers of land-survey sections, we find a decreasing area of Madia from north to south in 1936, as follows:

TIER	*Total Acres*	*Acres Madia*	*Percent area*
S11, 12, 7, 8 (T14S)..	2,560	2,430	95
S14, 13, 18, 17	2,560	2,420	95
S23, 24, 19, 20	2,470	2,170	88
S26, 25, 30, 29	2,560	1,230	48
S35, 36, 31, 32	2,560	1,410	55
S2, 1, 6, 5 (T15S)	2,450	1,280	52
S11, 12, 7, 8	2,560	380	15
S14, 13, 18, 17	2,560	810	32
S23, 24, 19, 20	2,540	480	19
S26, 25, 30, 29	2,510	90	4
S35, 36, 31, 32	2,510	0	0

The spread of Madia is further attested by the

fact that in the course of recent field work in this same territory it has been found in abundance where it was not reported in the 1936-38 range survey. Its spread since 1942 in an ephemeral community has also been observed near the site of a sheep camp in the head of Ephraim Canyon. In this case it is clear that sheep were instrumental in its dissemination.

Farther south, on the ridge between the South Fork of Manti Canyon and the North Fork of Sixmile Canyon (S25, T18S, R3E) several large Madia patches were found in 1949. No Madia was recorded here either in the 1913 or 1937 range surveys. The 1937 survey gave a poorer vegetal composition for the type than the earlier survey, including 25% Polygonum and 30% Taraxacum, which undoubtedly prepared the way for successful establishment of Madia before 1949.

Wherever Madia has been found in quantity, persistent perennials have been previously eliminated. In comparing range surveys, for example, many types that had been dominated by Polygonum and other ephemerals in 1913-15 were dominated by Madia in 1936-37. In some instances Madia has been found as a minor component of perennial types, occurring in small openings. These instances are rare, however, and it is probable that persistent perennials can eliminate Madia completely. No instance is known where Madia has invaded a tall, dense stand of perennials.

The competitive ability of Madia is manifest. Until recently, attempts to seed perennial grasses into it on the Manti and Uinta National Forests have almost always failed. If the Madia is weeded before it has a chance to fruit, however, excellent stands of grass are obtained.

The fact that Madia is so strong a competitor is readily explained by its early and aggressive root growth. Its seeds germinate beneath as much as 12 in. of snow. Root lengths of Madia under snow were measured with the help of A. Perry Plummer on May 1, 1943, which varied from 22 to 55 mm, and averaged about 30 mm. At this time *Polygonum douglasii* had also germinated and was growing fast. Seedlings of grass that had germinated the previous fall were just beginning to grow. Where snow had been gone possibly as much as a week, Madia roots varied from 53 to 70 mm in length, and averaged about 60 mm. Here grass grains that had failed to sprout the preceding fall were just beginning to germinate.

It has been shown in the laboratory that Madia secretes a germination- and growth-inhibiting substance (Parker 1949-1950), which may help explain the slowness of invasion by perennials into Madia stands and the apparent ability of Madia to dominate other annuals. The inhibitory effectiveness of this substance has not yet been demonstrated under field conditions, however.

Madia roots go deeper than one might suppose from the size of the tops, although it is difficult to trace these delicate roots to their full length. In midsummer, 1942, a core of earth about 45 cm deep was dug from a stand of Madia. By careful washing with a spray of water in the laboratory a root at least 29 cm long on a plant with an 8-cm top, and another root at least 33 cm long on a plant with a 9-cm top, were obtained. The end of neither root had been reached. They may well have extended as far as 50 cm, for many unidentified roots were severed in lifting the soil core out of the ground. Sampson (1919) gives minimum, optimum, and maximum root lengths for Madia of 4, 7, and 10 in. (10, 18, and 25 cm). The maximum value is certainly an underestimate.

In summary, Madia puts its taproot down very rapidly, preempting soil moisture near the surface in spring before perennial grasses are able to use it, and probably keeping ahead of the roots of seedling grasses at lower levels. Where Madia grows thickly —at densities greater than 100 plants/sq m, say— grass seedlings are under a severe handicap. Furthermore, as the season advances, the soil is completely occupied to considerable depth by Madia roots. It is little wonder that perennials are slow in replacing such a competitor, particularly where they are handicapped by heavy grazing.

Succession

Evidence has already been presented to show that Madia invades bare areas or areas dominated by ephemeral species, and not areas having a dense cover of perennials.

Perennials, particularly *Agropyron trachycaulum, Bromus carinatus,* and *Stipa lettermani,* are known to invade stands dominated by Madia and in time to suppress it. When quadrats 62 and 63, established in 1914, were reexamined in 1942 and 1948, Madia was still dominant, with Polygonum, Collomia, and some other annuals also abundant (Table 28). However, Agropyron and Bromus had invaded the stand. Their seed source, obviously, had been from grasses under nearby aspen forest where Madia is absent. This invasion, while facilitated by the nearness of a seed source, was made in the face of severe sheep grazing. Although basal leaves of these grasses have been observed in late summer to be consumed by sheep, culms and heads were not destroyed, and presumably the grasses were able to seed successfully. (Neither Madia nor Polygonum were observed to have been grazed.) Invasion by grass here is very slow, but if grazing is lessened the eventual triumph of grass over Madia seems certain.

An example of replacement of Madia by perennials and of seesawing dominance under severe grazing and trampling is found at the southern end of the plateau in Gunnison Valley, S14, T20S, R3E. Here two 10 x 10 m major plots were established in 1919 on deep soil sloping 3% southwest. Judging from some of the species present—*Carex festivella, Erigeron ursinus, Plántago purshii, Epilobium hornemannii*—this site was at one time a wet meadow, but it now seems as dry a site as any occupied by upland forbs and

grasses. The area has been very heavily grazed for years by sheep, cattle, and horses, and sheet erosion has been going on since before the plots were established.

In a range survey of Gunnison Valley in 1914 no Madia was noted, which suggests that the plant was scarce or perhaps had not been introduced. In a second range survey in 1937, the plot area was part of a type occupying 1,060 acres and containing 11% Madia. When the plots were established in 1919, Madia made up 62 and 63% of their cover. By 1925, it made up only 1 and 2% of their cover. One of the plots was fenced in 1925. In 1940 a very little Madia was found on the fenced plot, on soil thrown up by pocket gophers, but it was rather conspicuous on the outside range generally. By 1949 the fence had been destroyed and the formerly fenced plot was heavily grazed and trampled: Madia made up 30% of its cover but at this time only 2% of the cover on the outside plot. These variations probably reflect local variations in grazing intensity and soil disturbance.

Thus the history of Madia in Gunnison Valley appears to be: (1) introduction possibly after 1914, (2) abundance by 1919, and (3) possibly a general decline in abundance, or fluctuating abundance, since. Madia is still dominant on considerable tracts, evidently maintained by overgrazing of perennial species and trampling of the soil.

Erosion-Pavement Communities

Accelerated erosion pavement of limestone fragments is very common on sites of naturally high erosion potential in the subalpine zone. These are principally shoulders and upper slopes of ridges (as on the Skyline and Wagon Road Ridge), and on ridges exposed to wind, as on Tent Mountain and White Mountain. The dividing line between what is natural and what is accelerated erosion pavement is still to be drawn. From evidences of accelerated erosion associated with most areas of erosion pavement (persisting soil remnants, "stilted" shrubs, gullies incising the soil mantle on lower slopes), it is concluded that areas of natural erosion pavement were not extensive on pristine range. They probably consisted of narrow strips along the shoulders of ridges that break away into cliffs, parts of semi-stabilized talus slopes, and pockets of developing soil in rock piles (Fig. 12). Taken together such areas would not make up more than a fraction of a percent of the subalpine zone. The area of accelerated erosion pavement today is probably on the order of 5%.

SOIL

A close view of an accelerated erosion pavement formed from colluvial material is given in Fig. 35. Part of the solum remains at right because the surface has been protected from overland flow by the *Ribes inebrians* bush upslope from it. At a greater distance from such protection, as in the center, all surface soil has been lost, leaving an erosion pavement of limestone fragments. Stripping off all the fine material in this way amounts to setting the clock back some hundreds or thousands of years, exposing the kind of parent material from which the soil was originally developed.

FIG. 35. A roadcut near the head of Ephraim Canyon, showing formation of an erosion pavement from colluvial parent material. Soil mantle at extreme right has been most protected from erosion because of the currant bush on the slope above. Scale is given by meter stick. Elev. 10,000 ft. October 19, 1944. F-434392

A soil profile under erosion pavement on residual parent material is shown in Fig. 15.

During intense rain storms, erosion-pavement areas do not give rise to surficial runoff anywhere nearly so readily as areas of bared soil. In fact, streams of water that collect and become concentrated on bared soil and that debouch on pavement tend to be absorbed. The rocks check the rush of water, which spreads, dropping part or all of its silt load. This conservative effect is naturally less marked as storm intensity and volume increase. Thus, although erosion pavement may be considered a kind of protective scar tissue, its presence does not mean that accelerated erosion has been stopped.

At least three agencies expose fine particles to the chance of loss, either by wind or water, thus deepening the erosion pavement. These agencies are livestock, which disturb the surface by trampling, pocket gophers, which bring loose soil to the surface (Ellison 1946), and frost, which elevates the fine particles above the gravel.

As a general rule stabilization by vegetation appears to be an extremely slow process. Figure 36 contrasts erosion pavement under grazing (or, rather, trampling, since there is little vegetation to graze) with a comparable area of pavement that has been under partial protection for some 30 years. The larger grass tufts are strongly elevated on little islands of fine soil material, while smaller (and younger) tufts are less elevated. The pedestalling of these grasses is not to be accounted for by supposing them to be frost-heaved. I have often observed the effects of frost heaving on such sites, and it has always been the intervening spaces, not the grass tufts, that have been disturbed. The pedestalling is evidently a result of erosion of soil particles from

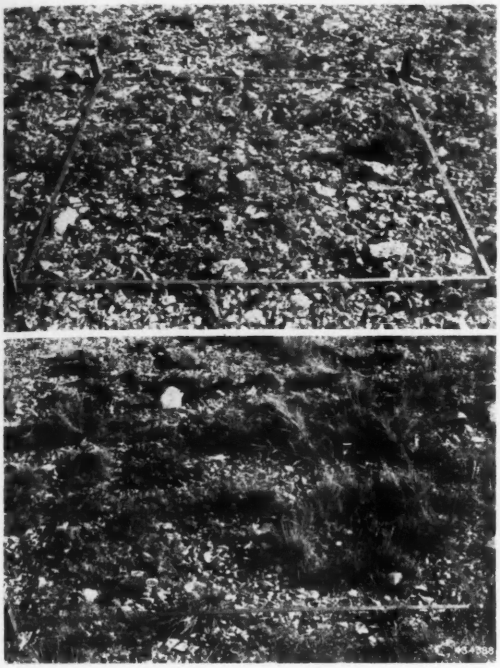

FIG. 36. Meter-square quadrats on erosion pavement of currently grazed and trampled range (above) and on comparable range that has been grazed seldom during the last 30 years. Nearly level ground with a slight westerly exposure, head of Ephraim Canyon, 10,200 ft. elev., October 18, 1944. F-434389, F-434388

the interspaces (and some deposition in the grass tufts) which results in a gradual sinking of the gravel-covered surface.

The grass tufts die in course of time, and the fine soil particles they protect are usually exposed and washed or blown away. Several such tufts are visible in the two quadrats in Fig. 36. Sometimes these islands of soil are successfully colonized by other plants, but apparently not often. This suggests that height of the pedestal is a limiting factor in plant establishment and survival: the higher the pedestal, the greater the hazards of drying and heating of the soil.

LESQUERELLA-ERIGERON-FESTUCA COMMUNITY

Vegetation on erosion-pavement areas is scanty. Percentage cover of three of the stands described in Table 29 is as follows:

	60	*61*	*955*
Vegetation	14	12	14
Litter	9	T	12
Rock and gravel	51	66	62
Bare soil	26	22	12

This vegetation is a mixture of species that appear on a well-developed soil mantle and those characteristic of naturally developed erosion pavement early in primary succession. The former are found mostly where soil deterioration has been least severe

TABLE 29. Vegetal composition of four erosion-pavement stands representing the Lesquerella-Erigeron-Festuca community.* Abundance symbols are explained on page 92.

Stand No.	60	61	905	995
Grasses				
Agropyron trachycaulum	1	1	1	x
Bromus carinatus	..	..	x	
Festuca ovina	3	2	1	1
Poa fendleriana	4	4	x	1
P. palustris	1	..	x	2
Stipa lettermani	x	x	1	
Trisetum spicatum	..	..	1	
Perennial forbs				
Achillea lanulosa	1	1	4	x
Anemone globosa	R	..	..	3
Antennaria arida	1	1		
Aquilegia coerulea	..	..	x	
Arenaria sp.	..	..	x	
Artemisia discolor	x	x	2	
Astragalus carltonii	x	x	x	2
Erigeron compositus	3	2	1	2
E. speciosus	..	..	..	R
E. ursinus	..	..	x	
Frasera speciosa	..	..	..	x
Gilia pulchella	x			
Lathyrus lanszwertii	..	..	x	
Lesquerella utahensis	2	2	2	1
Penstemon rydbergii	..	..	x	
P. subglaber	..	..	..	3
Polemonium foliosissimum	x	..	x	
Potentilla (pulcherrima?)	1	1	x	1
Pseudocymopterus montanus	3	3	1	3
Ranunculus inamcenus	..	..	x	
Sedum stenopetalum	..	..	..	2
Senecio cymbalaroides	..	..	..	1
Smilacina stellata	..	..	x	
Taraxacum officinale	1	4	1	x
Thalictrum fendleri	..	x	x	
Townsendia montana	2	1	x	
Vicia americana	x	..	x	
Annuals				
Androsace septentrionalis	..	R	x	x
Shrubs				
Chrysothamnus viscidiflorus	..	..	x	
Juniperus communis	..	..	x	
Mahonia repens	..	..	x	
Ribes inebrians	x	x	1	x
R. montigenum	x	x	1	
Symphoricarpos oreophilus	..	..	x	

*Stand 60. Head of Ephraim Canyon, inside Erosion Area A, T17S, R4E, S26, 10,200 ft. elev. Ungrazed.
Stand 61. Same, but on outside Erosion Area A. Trailed and grazed by sheep.
Stand 905. Near John August Lake, T17S, R4E, S35, 10,300 ft. elev. Grazed by sheep.
Stand 995. Head of Manti Canyon, T18S, R4E, S10, 10,000 ft. elev. Grazed by cattle.

—on the most severely eroded sites sometimes only as relics under shrubs. For example in stand 905 *Bromus carinatus* and *Penstemon rydbergii* were found on soil remants and on accumulations of soil in the lee of currant bushes. *Polemonium foliosissimum* was found on soil at the edges of currant bushes in both stands 60 and 905. The species most characteristic of erosion pavement in Table 29 are:

Festuca ovina	*Lesquerella utahensis*
Poa spp.	*Potentilla* sp.
Astragalus carltonii	*Pseudocymopterus montanus*
Erigeron compositus	*Townsendia montana*

Other species, less constant in Table 29, but distinctive in an erosion-pavement environment are *Anemone globosa* and *Sedum stenopetalum*. The appearance of this community is well shown in Fig. 36.

The outstanding difference in vegetal composition between stands 60 and 61 is the greater abundance of Taraxacum on the grazed range. If the percentage of Taraxacum in each stand (estimated inside, at the midpoint of class 1, as 2.5%, and directly estimated outside to make up 25% of the cover) be multiplied by the respective percentages of total cover, we have:

Inside (Stand 60): .025 x .14 = .0035
Outside (Stand 61): .250 x .12 = .0300

as absolute values. In other words, there is almost 10 times as much Taraxacum under heavy grazing as under protection. The spreading habit of the Taraxacum is largely responsible for the apparent similarity in amount of cover between this stand and the protected stand.

LOMATIUM COMMUNITY

An erosion-pavement community dominated by *Lomatium nuttallii* is often noted in the subalpine zone (Fig. 37). Lomatium may appear to form almost pure stands, but usually other erosion-pavement species, such as *Gilia pulchella*, *Eriogonum neglectum*, and *Festuca ovina* are present as an understory. A description of an erosion-pavement community on a level site where primary succession appears to be under way is given on page 120; in this, Lomatium makes up 25% of the cover. Where a series of knolls or ridges has been formed as by ancient slumps, erosion resulting from overgrazing has left pavement on the convex slopes in alternation with deeper soil in the depressions; and correspondingly Lomatium-dominated erosion-pavement communities alternate just as sharply and repeatedly with more mixed upland-herb communties.

IVESIA COMMUNITY

A distinctive community favored by severe accelerated erosion is one dominated by *Ivesia gordonii*. Where Ivesia is abundant associated species are scarce, even though there may be rather large bare areas between Ivesia plants (Fig. 38).

FIG. 37. Type change between Lomatium community on erosion pavement, left, and communities on deeper soil. Note remnants of soil in the erosion pavement. As erosion continues, pavement and Lomatium will extend farther up slope to right. Dominants in foreground are Viola, Stipa, Artemisia, and Geranium. Ephraim Canyon, elev. 10,200 ft. August 24, 1950.

FIG. 38. Pedestaled *Invesia gordonii* on a site where erosion pavement is heavy. Skyline, near West Sanpete Mountain, essentially level terrain, 11,000 ft. elev. October 11, 1940. F-416003

Ivesia is not widely distributed on the Wasatch Plateau. It occurs abundantly in the vicinity of Sanpete Peak (S6, T17S, R5E), and is also to be found on Wasatch Peak (S34, T19S, R4E). Under natural conditions it appears to be a crevice plant, a member of the alpine relic community, but following widespread accelerated erosion it has invaded not only areas of exposed bedrock, but areas of erosion pavement and even areas of bare soil where erosion pavement is not yet well developed.

The tendency for Ivesia to increase as erosion progresses, reducing vegetal cover and exposing rock, is illustrated by the abundance of this species in three stands of *Artemisia rothrockii* (Table 27).

That Ivesia has spread in recent years is clearly evident in the field. Stands of Ivesia are particularly large and distinctive along the Skyline at the head of Horseshoe Flat (T17S, R5E), which is the headwater drainage basin for Littles, Olsen, and Beeks Creeks. Horseshoe Flat, an area of about 6,500 acres, has been eroded more severely, probably, than any other single area of comparable size on the plateau. In places acres of bare bedrock, showing characteristic subsurface weathering, are exposed, stripped of all soil (Fig. 39). On slopes nearest the Skyline, where denudation has been most complete, Ivesia prevails. But individual stands become progressively smaller and less pure eastward as less completely eroded soils are encountered. Here Ivesia is conspicuous only in rock crevices and on gravel bars of the scoured drainage channels. The conclusion is easily drawn that this plant has migrated eastward along these drainageways from the Skyline. The progressive thinning of Ivesia as one ascends the adjacent slopes, and a parallel shift toward predominance of younger age classes, also indicate that Ivesia has spread and is spreading from the drainage channels to intervening slopes and ridges.

FIG. 39. Limestone bedrock exposed by accelerated erosion. Judging from the site, original soil mantle was deeper than that shown in Fig. 16. Vegetation on islands of soil behind camera case and in middle distance is mainly Stipa and Penstemon. Dark, hummocked plants are Ivesia. Horseshoe Flat, S11, T16S, R4E, Elev. 10,500 ft. August 28, 1948. F-464243

SUCCESSION

That the majority of erosion pavements have been derived from former soil mantles is clear. The evidence is found in associated signs of erosion that is obviously accelerated. These signs occur both in all stages of destruction of a soil mantle (and corresponding pavement development) and in remnants of soil that often occur as elevated outliers, separated from each other and from a nearby soil mantle by areas of erosion pavement.

The soil profile and vegetation of strongly developed accelerated erosion pavement bear a striking resemblance to the young profile and corresponding vegetation of an early stage in normal succession. This early stage is one in which the position of parent material is stabilized and crevices between rocks are filled with organic soil (Figs. 12, 15).

While trends *toward* accelerated erosion pavement are clear, because evidence for them is abundant, the mechanics of succession *from* accelerated erosion pavement to a normal soil mantle are necessarily in doubt. One bit of evidence is the change during 30 years' protection on one fairly level site, which has been described (Fig. 36). A few repeat photographs show that shrubs, particularly *Ribes inebrians* and *R. montigenum*, become established on areas of accelerated erosion pavement (Fig. 40), and occasional young trees of Engelmann spruce and alpine fir may be found on such sites. It is also known that, on areas where erosion pavement is not strongly developed, the upland-herb species of nearby deeper soils invade if grazing is lessened or excluded. The supposition is therefore reasonable that the course of succession on accelerated erosion pavement will vary from that of secondary succession on deeper soils to that of primary succession on areas of natural erosion pavement. Few pavement areas give evidence of real soil stability at the present time, however.

It is evident that stabilization of erosion pavement is finally to be achieved as a result of a balance among several factors in an intricate play of forces. An increase of rock on the surface favors stabilization, and so does an increase of vegetation. Presumably these two factors alone bring about eventual stabilization, yet the two are essentially antagonistic. As fine particles continue to be lost the layer of rocks becomes deeper, protecting the remaining particles yet at the same time making establishment of herbaceous vegetation more difficult. Full stabilization cannot be achieved, so that primary succession can really begin, unless the establishment of vegetation becomes aggressive enough to prevent loss of particles and slipping and sliding of rocks. The fact that woody plants can become established naturally on erosion-pavement slopes suggests that main reliance might well be placed on shrubs and trees in artificial planting rather than on the herbaceous species with which most research has been done up till now.

In any event it must be recognized that the process of soil-mantle development from a heavy erosion pavement can be reckoned in terms not less than centuries. It is an infinitely slower process than the secondary successions on denuded soils that have been described in the preceding pages.

FIG. 40. An eroding slope with a developing erosion pavement in 1910 (above) and in 1948. Some new bushes of *Ribes inebrians* have appeared: one of the larger stems of the new bush in the middle of the slope had 16 growth rings in 1948. The trees that have appeared on the bench (right center) are growing from a clump of Sambucus where some old logs are lying on the ground. Near Seely Creek Guard Station, T17S, R4E, S25. Elev. 9,800 ft. F-94980, F-464244

DISCUSSION: THE INFLUENCE OF GRAZING

It will be well at this point, having described the major communities included in the upland-herb association and the changes this association has undergone as a result of grazing, to summarize the effects of grazing and relate the communities to one another. This section is therefore concerned with bringing the loose ends of the evidence together into a coherent appraisal of the grazing factor.

Grazing cannot be evaluated fairly, however, because *overgrazing* has been the rule. Practically all grazing in the subalpine zone of the Wasatch Plateau has been so severe as either to destroy the cover or to reduce it so that erosion has been greatly accelerated. In those relatively small areas where accelerated erosion is not a factor, accelerated deposition may be. We do not know what the full effects of light or moderate grazing might be, because they have never been tested in a controlled experiment over a sufficiently long period to show significant results. There is some evidence, wholly observational in character, to suggest that light or moderate grazing may be as beneficial as complete protection. At any rate, parts of the grazed range in the head of Ephraim Canyon appear to be making as rapid progress toward an effective vegetal cover as comparable parts of the protected Alpine Cattle and Carrying Capacity Pastures.

An important fact to be kept in mind in visualizing changes that have occurred in the subalpine zone of the Wasatch Plateau is that the original herbaceous vegetation was practically destroyed by abusive grazing in the 1880's, 1890's, and early 1900's. Available reports (Reynolds 1911), and evidence on the ground of accelerated erosion on a vast scale, bespeak denudation of the soil and virtual elimination of the native forbs and grasses. There were some areas more difficult for livestock to reach which were less denuded than the subalpine zone as a whole, but probably these were neither large nor numerous; these may be the areas that today are in best condition. With loss of the original plants and their inability to become reestablished, either because of lack of a seed source, destructive grazing of the seedlings, or erosion of the topsoil, the ground was evidently taken over by ephemeral and ruderal species. There was probably little time or opportunity for orderly replacement of the original community by a series of communities successively more resistant to grazing. The communities we have today, therefore, do not represent the change that selective grazing would have made in the original upland-herb association: they represent the plants that have been introduced, and the natives that have been able to increase, beginning with a drastically altered microenvironment and continuing under the pressures of selective grazing.

SECONDARY SUCCESSION

It will be profitable to consider the well-known successional concept developed by Sampson (1919) for the subalpine zone of the Wasatch Plateau, in order to contrast with it the concept developed here. Sampson grouped the herbaceous communities, excluding those of wet meadows, into four stages, as follows:

"The wheat-grass consociation (subclimax stage).
"The porcupine-grass-yellow-brush consociation (mixed grass-and-weed stage).
"The foxglove-sweet-sage-yarrow consociation (second or late weed stage).
"The ruderal-early-weed consociation (first or early weed stage)."

Sampson considered the "wheat-grass consociation" to be the climax herbaceous cover, but subclimax to forest. This point has been dealt with in a previous section (p. 110). He believed that severe grazing pressure would bring into being communities lower in this scale ("retrogressive succession"), while relief from such pressure would restore those higher in the same scale ("progressive succession"). He recognized that, below the "first weed stage," severe erosion would destroy all the soil and expose bare rock.

Stages of secondary succession as developed in the present study are given in Fig. 41.

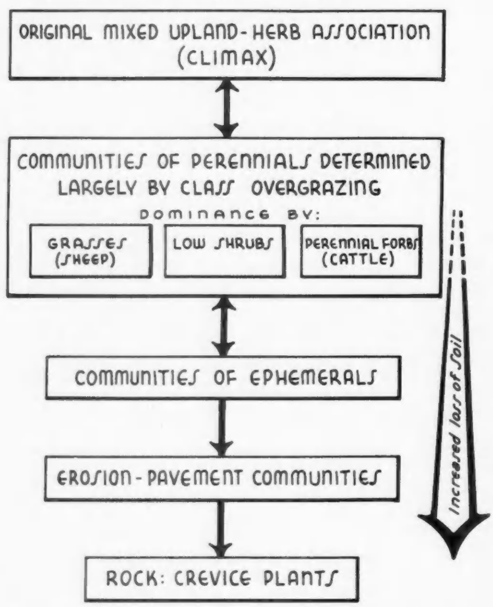

FIG. 41. Scheme of secondary succession on upland-herb sites as influenced by grazing pressure. Accelerated erosion is a major factor in bringing about the two lowermost stages, erosion-pavement communities and rock; the one-way arrows indicate it to be an irreversible process.

Dominance by Ephemerals

"Ephemerals" have been defined as annuals, early withering perennials, and ruderals or near-ruderals. Ephemeral communities persist where grazing and trampling are severe. If *Madia glomerata* is introduced, this species commonly assumes dominance over

the others. Although itself an annual, Madia is such a strong competitor against perennials when these are handicapped by heavy grazing that it may remain dominant for many years, only slowly giving way to perennial species as grazing pressure is lessened.

From these ephemeral communities, most of the secondary succession in the subalpine zone has stemmed. In some instances considerable fertile topsoil remained at the time our records began, and the growth of annuals was dense (e.g., Becks Ridge); in others only subsoil was left, and the growth, even of annuals, was sparse (e.g., Bear Creek). In the main these communities correspond with Sampson's first weed stage, although a number of species (*Viola nuttallii, Oenothera flava, Delphinium nelsonii* et al.) are included in his early second weed stage.

Dominance by Grasses

Although dominance by a number of grasses may reflect heavy grazing by sheep—*Agropyron dasystachyum, Agropyron trachycaulum, Hesperochloa kingii,* and others—the most usual dominant on heavily grazed sheep range is *Stipa lettermani. Agropyron trachycaulum, Stipa columbiana,* and *Trisetum spicatum* often occur with it as minor constituents. Certain forbs may be conspicuous in these "grass-dominated" communities, notably the ubiquitous *Taraxacum officinale* and the rhizomatous species *Achillea lanulosa, Artemisia discolor,* and less commonly, *Penstemon rydbergii.* The absence or scarcity of other grasses and sedges—*Bromus anomalus, Poa fendleriana, Carex festivella,* for three—is significant, as is the absence or scarcity of forbs like *Mertensia leonardi, Osmorhiza occidentalis, Valeriana occidentalis, Geranium richardsonii, Polemonium foliosissimum,* and *Erigeron speciosus.* These scarce grasses and forbs which are now found as relics represent a class of tall, mesic species very different in aspect from the xeric grassland that characterizes sheep range today. The trend from ephemerals to grasses under heavy grazing by sheep has included, therefore, a tendency for continued xerophytism.

Under heavy grazing and trampling, the plant cover is lessened, forbs like Taraxacum and ephemeral species may be more prominent than the grasses, and evidence of active erosion may be conspicuous. Judging from quadrat records, the well-marked trend in which grasses have replaced ephemerals on sheep range in the Mile Strip has now ended and the present intensity of sheep grazing is, at best, holding the vegetation at a standstill. There has been a slight but consistent tendency for increase of ephemerals, ruderals, and species of low forage value. On most slopes accelerated soil erosion is still rapid. So far as is known, management practices have not changed materially for the worse in recent years. This suggests, then, that practices effective in achieving a certain improvement may be wholly inadequate to insure its continuation.

In some Stipa-dominated communities that appear to be grazed less heavily, mesic forbs and grasses are appearing. In some instances these plants are clearly derived from relics in the shelter of nearby shrubs. Future trend under reduced grazing by sheep, therefore, would be toward a more mixed, mesophytic cover.

In Sampson's successional scheme these grass-dominated communities lie either in the mixed grass-and-weed stage or, where Agropyron predominates, in the subclimax wheatgrass stage. As Fig. 41 shows, these are regarded as essentially equivalent to communities dominated by low shrubs or by perennial forbs, all being modified by class overgrazing.

Dominance by Low Shrubs

It happens that increase of the low shrubs, *Chrysothamnus viscidiflorus* (yellowbrush) and *Artemisia rothrockii* (sagebrush), has occurred chiefly on range heavily grazed by sheep rather than on range grazed by cattle. The origin of these shrub-dominated communities seems to be the same as the origin of grass-dominated communities: denudation of the original cover and dominance of ephemeral species, followed by invasion of persistent perennials—in this case, low shrubs. As with *Stipa lettermani,* the increase of Chrysothamnus and Artemisia has evidently been helped, not only by destruction of the original mesophytic herbaceous cover but by the general spread of xeric conditions accompanying overgrazing and accelerated soil erosion.

Although some stands of these low shrubs include abundant herbaceous vegetation and provide effective soil protection, there are heavily grazed stands where soil is eroding rapidly and change is toward erosion pavement. Trend in this direction is the same for low-shrub as well as herbaceous communities, therefore. How or whether the shrubs would be replaced by other vegetation under light grazing or complete protection is only conjectural. Whether Chrysothamnus can be eliminated by competition of herbaceous species has yet to be proved: it has maintained itself under protection for nearly 40 years. Whether it can be eliminated by fire is not known. The fact that it has been found sprouting from the root in a roadcut suggests that it may be fire resistant. Fire cannot be much of a factor so long as grazing, which eliminates most of the potential fuel, is as intensive as at present. It appears, therefore, that *Chrysothamnus viscidiflorus,* which has increased greatly since settlement, will remain a conspicuous plant in the subalpine zone of the Wasatch Plateau for a long time.

Sampson (1919) did not include the sagebrush community in his successional scheme, doubtless because, compared with the yellowbrush community, it did not cover much area. The yellowbrush community corresponds to his "porcupine-grass-yellowbrush consociation." The evidence that has been presented indicating spread of Chrysothamnus during the past 50 to 60 years corroborates Sampson's observation that this species increases with overgrazing.

Counts of growth rings and records of persistence of bushes on mapped plots demonstrate that he greatly underestimated the longevity of this species (1919, *p. 15*). Its persistence, undiminished and flourishing, in at least three areas protected from grazing for periods of from 32 to 38 years, indicates that it is not readily killed by competition from either Stipa or Agropyron, as he believed (1919, *pp. 28-29*).

The evidence at hand also indicates that Sampson was incorrect in placing the Chrysothamnus-Stipa community in an intermediate position between the "second weed stage" and the climax. If it were successionally intermediate (accepting for the sake of argument Sampson's concept that "progressive" and "retrogressive" succession follow the same path but in opposite directions), one might expect to find evidence as follows:

1. Chrysothamnus-Stipa stands on heavily grazed range should show signs of being replaced by "second weed stage" species. On the contrary, yellowbrush persists under heavy grazing, either by sheep, or by cattle, or by sheep and cattle together. Some stands are grazed and trampled so severely that the soil is being reduced to rock and gravel between the shrubs, and the shrubs themselves are being undermined. The shrubs hang on as long as there is soil left to support them, and when this is gone and the shrubs are gone the only vegetation remaining is an erosion pavement community.

2. Relics of Chrysothamnus should be found in some areas dominated by Penstemon and other "second weed" species on overgrazed range. That the wood of Chrysothamnus will persist for many years is proved by its persistence when buried by wind-deposited soil, and by the evident age of dead and dying stubs and branches above ground. But on "second weed" areas such relics have not been found, either as very old living plants or as dead stubs.

3. On lightly grazed or completely protected range, the trend from "second weed stage" should be toward Chrysothamnus and Stipa, and eventually toward the "wheatgrass consociation." Actually the trend is toward a mixture of many species of grasses and forbs. The Alpine Cattle-Pasture, Carrying-Capacity Pasture, and Elk Knoll, grazed and protected in varying degree and for different periods, provide consistent evidence on this point. They indicate a trend toward a mixed forb-grass community like that in the natural areas that have been found in the subalpine zone of the Wasatch Plateau.

In short, the evidence that has been presented leads to the conclusion that the yellowbrush community is not different in successional rank from grass-dominated communities on sheep range or from forb-dominated communities on cattle range. The sagebrush community is probably another equivalent. All these communities are believed to lie in an equally intermediate position between communities of ephemerals at the lower end, and the mixed upland-herb association at the upper end, of the secondary successional scale.

Dominance by Perennial Forbs

Trend on heavily grazed cattle range has differed in detail from trend on heavily grazed sheep range in that grasses (which as a class are grazed more eagerly by cattle than by sheep) are suppressed and certain forbs have assumed dominance. Universally dominant forbs are *Taraxacum officinale* and *Geranium richardsonii,* and some of the local dominants are the same rhizomatous species that are locally abundant on sheep range, notably *Artemisia discolor, Achillea lanulosa,* and *Penstemon rydbergii.* But while differing in detail from trend on sheep range, a similar tendency toward maintenance of xerophytism is manifest. Bare soil surface is exposed and most of the taller forbs and grasses are reduced to relics.

The invasion of ephemeral communities by these rhizomatous species is clear because it is possible to infer relative ages of these plants from their areal spread, their compactness and height, and the extent to which they have been pedestaled by erosion. Invasion by taprooted species like Geranium and Lupinus on heavily grazed range can be inferred from similar evidence. With reduction in grazing pressure, as at increasing distances from water or under protection from grazing, invasion by more palatable forbs and even grasses—*Erigeron speciosus, Castilleja sulphurea, Valeriana edulis, V. occidentalis, Bromus carinatus, B. anomalus, Agropyron trachycaulum*—is also manifest.

Forb-dominated communities correspond to Sampson's "foxglove-sweet-sage-yarrow consociation" or second weed stage, although it appears from his description that Taraxacum and Geranium were much less abundant in these communities 35 or more years ago than they are now. Forb-dominated communities may well precede grass-dominated communities in certain instances, as was noted in the stabilization of the soil surface in upper Bear Creek by Achillea prior to invasion of forbs and grasses by seed; but this precedence is not always necessary, and in my opinion the two classes of communities are essentially of equivalent rank. Each represents a successional transition, colored by the influence of selective grazing, between the ephemeral communities of denuded surfaces and the original, mixed upland-herb association.

Although grasses are strongly suppressed by heavy cattle grazing, they do not increase so aggressively under protection as to suggest their eventual dominance over tall forbs. The slight change in grasses in 20 years of partial to complete protection from cattle grazing in the Alpine Cattle-Pasture is an example. The 11 Alpine Cattle-Pasture quadrats obviously were intended to represent Sampson's second weed stage since *Penstemon rydbergii* was dominant on all of them at the time of establishment, or perhaps a transition toward his first grass stage since *Stipa lettermani* was also present on all of them. They have shown no tendency toward suppression of the second weed stage forbs by Stipa or Chrysothamnus (there is an ample supply of seed of the latter

above and to windward of the Alpine Cattle-Pasture), and no tendency to approach a wheatgrass-dominated climax. The tendency they do show is toward a mixed forb-grass community, in which Agropyron, Melica, Bromus, and *Stipa columbiana* may be locally dominant, but in which for the most part they are co-dominant with many species of forbs.

DESTRUCTIVE CHANGE

Accelerated erosion has commonly accompanied the changes that have been described under secondary succession because of reduction in plant cover through overgrazing. Accelerated erosion is not a necessary concomitant, however: destruction of the upland-herb community leading to communities of ephemerals, and replacement of these by perennial grasses or forbs, as on parts of Toms and Becks Ridges, probably took place without a great deal of soil loss. But on sloping ground there has commonly been material loss of soil by accelerated erosion, and despite considerable improvement in vegetation in many places this process is still going on.

Dominance by ephemerals or the occurrence of scattered plants of Geranium and Taraxacum on rapidly eroding ground has led to the assumption that these species indicate a natural stage in "retrogression" and only they can grow on soils so greatly depleted. This is putting the cart before the horse: this kind of vegetation is not present because the soil is eroded so much as the soil is eroding because this kind of vegetation gives it inadequate protection. Research in artificial revegetation has shown that many of these same soils, if plowed, planted, and given reasonable protection from grazing, will support dense stands of perennial vegetation.

It is true, of course, that accelerated erosion modifies the site very greatly and that the conditions accompanying it have a great deal to do with the kind of vegetation that succeeds in becoming established (Ellison 1949a). Furthermore, because of the difficulty that plants have in getting established on some eroded slopes, the soil may continue to erode long after overgrazing is removed. Cause and effect, therefore, may be widely separated: the subalpine zone of the Wasatch Plateau is still suffering from abuse it received 50 or more years ago. Put another way, it is often difficult to distinguish between trends that result from current grazing and trends set in motion by grazing, or by other factors, in the distant past. This is one of the major problems in judging range condition and trend.

There is abundant evidence to show that accelerated erosion can go on independently of vegetal composition. Accelerated erosion is usually conspicuous in ephemeral communities, because the soil is essentially bare after midsummer, but it also occurs in grass-dominated communities, in forb-dominated communities, and in communities dominated by low shrubs—wherever cover is sparse. The dominance of the bunch wheatgrass *Agropyron trachycaulum* on the rapidly eroding Bear Creek plots, even though this species is believed to have been a constituent of the original mixed upland-herb association and though Sampson considered it to have been the essential climax dominant, is a striking example of this fact (Ellison 1943). This independence of accelerated erosion and plant composition, which is of utmost importance in the application of ecology to land use, has been recognized by segregating accelerated erosion from secondary succession under the name "destructive change" (Ellison 1949b; Ellison, Croft & Bailey 1951).

Thus in judging range condition and trend in relation to the normal or pristine, plant composition alone is not a safe criterion. One must take into account not only the *composition* of the vegetation but, more particularly its *amount*, its adequacy as protective cover. Where plants and the litter between them cover less than 50 to 75% of the surface in the subalpine zone of the Wasatch Plateau, accelerated erosion is usually manifest.

Because of the erosion factor, bared soil and the dominance of ephemeral vegetation is by no means the nadir in possible deterioration. The exposure of bare bedrock, with plants growing only in crevices (Fig. 39) is the most extreme form. More commonly a less extreme form of deterioration is reached in the development of erosion pavement (Fig. 36) with an aggregation of species resembling that in early stages of soil formation and primary succession. Succession from this condition to a mixed upland-herb cover cannot be reckoned in terms of decades, as it may be where a soil mantle persists, but in terms of centuries or millenia, whatever time span may be required for development of a soil.

Sampson's (1919) successional scheme, which relates only to secondary succession on soils bared by overgrazing, involves an unfortunate confusion of primary and secondary succession, and misses the significance of destructive change. This confusion leads to the belief that with overgrazing and accelerated erosion, primary successional stages reappear in reverse order to that in which they appeared as vegetation and soil were initially developed (*loc. cit., pp. 3-6*). The fallacy of this concept is of more than academic interest. A realistic appreciation of the disparate time requirements for the two kinds of succession is of utmost importance to practical range-watershed management. The same may be said, and more emphatically, of the disparate time requirements for normal soil-forming processes and gelogic normal erosion as opposed to the visible, accelerated erosion that is common today on the Wasatch Plateau and many other subalpine range-watersheds of the West. It is ruinous for the range manager to be guided by a belief that vegetal changes associated with accelerated erosion are the counterpart of normal, primary succession, and that accelerated erosion is merely the counterpart of normal soil development.

LIMBER-PINE COMMUNITY

A xerophytic forest community, dominated by limber pine (*Pinus flexilis*), is found on steep, south-facing slopes (Fig. 2: *40, 87-90 ch. south*). It grows on rocky outcrops, forms an irregular and scanty fringe on edges of ridges, and continues down the faces of cliffs unless these are too steep to afford a foothold. In contrast to the spruce-fir association, the limber-pine community thrives on dry, warm exposures, and the trees, instead of colonizing talus, anchor themselves in crevices of bedrock. This happens usually to be limestone.

The sites occupied by this community are characteristically windswept. Because of wind, prevailingly warm exposures, and steep slopes, snow accumulation and persistence on these sites is less than on any others.

Natural erosion is rapid, and the only soil development is in crevices. Even though a soil mantle might have been developed originally in places with least erosion potential, grazing and trampling of livestock have destroyed it by now. Large tree roots are commonly exposed, even more gnarled than the contorted branches of the trees.

Often a few other trees—Douglas-fir (*Pseudotsuga taxifolia*), alpine fir and Engelmann spruce—are associated with limber pine. A scattered understory of shrubs may occur, and a very sparse growth of forbs and grasses. These, like *Erigeron compositus, Anemone globosa, Pseudocymopterus montanus, Festuca ovina,* and *Poa palustris,* have also become widespread on areas of accelerated erosion pavement.

The understory of a limber-pine community on the south side of Elk Knoll (T18S, R4E, S3; elev. 10,000 ft.) will serve as an example. This vegetation has probably not been grazed by livestock for 50 years; it is, however, easily accessible to deer and elk. The understory vegetal cover is sparse, averaging less than 5% of the area, and little litter occurs except accumulations directly under the scattered trees. The surface is mostly rock, either outcrops of bedrock, or natural erosion pavement. The average slope is 80%. Species by abundance classes (p. 92) are as follows:

Aster glaucodes	3
Monardella odoratissima	3
Castilleja viscida	3
Ribes inebrians	2
Symphoricarpos oreophilus	2
Mahonia repens	2
Poa palustris	1
Anemone globosa	1
Pachistima myrsinites	1
Lathyrus lanszwertii	1
Epilobium angustifolium	1
Smilacina stellata	1
Juniperus communis	1
Populus tremuloides	1
Senecio cymbalaroides	1
S. multilobatus	x
Artemisia discolor	x
Aquilegia coerulea	x
Bromus carinatus	x
Chaenactis douglasii	x
Geranium richardsonii	x
Penstemon rydbergii	x
Astragalus carltonii	x
Agropyron trachycaulum	x
Poa fendleriana	x
Achillea lanulosa	x
Rosa fendleri	x
Holodiscus discolor	R

Of the 28 species listed, 8 are woody, in addition to limber pine, Englemann spruce, and alpine fir. Two of these, Mahonia and Pachistima, are common in aspen and spruce-fir forests, together with the forbs Epilobium and Smilacina. Monardella, Castilleja, Aster, Anemone, Aquilegia, and Chaenactis are frequently found on rocky surfaces, the first two particularly on warm, southerly exposures. Thus these as well as the other herbaceous species commonly occur in other communities.

The limber-pine community is obviously primitive in the scale of primary succession because it lacks a soil mantle and occupies the most xeric sites in the subalpine zone. Beyond the fact that individual pines or groups of pines may be succeeded by other trees, notably alpine fir, no further successional development occurs on these sites. As the cliffs are reduced to talus, limber pine is destroyed; the talus is invaded by spruce and fir; and as a complete soil mantle is developed, these are replaced by tall shrubs and eventually the upland-herb association.

Limber pine and Douglas-fir show a tendency to invade upland-herb communities where accelerated soil erosion has been severe. This tendency is particularly evident on Wagon Road Ridge near the White Knoll (Fig. 42), but has been noted more widely (Stand 964, Table 27). Almost invariably the young trees are found beneath shrubs, usually currants, but often yellowbrush or sagebrush. This appears to be the only succession of consequence from herbaceous vegetation to forest that occurs in the subalpine zone of the Wasatch Plateau, and it is evidently not natural, but induced by overgrazing.

FIG. 42. Invasion of deteriorated stand of Chrysothamnus and Stipa—note erosion pavement—by limber pine and Douglas-fir. The parent trees in the limber-pine community at right occupy the ridge shoulder and steep south slope. (Conifers mingled with aspen in the distance are mostly alpine fir and Engelmann spruce.) Wagon Road Ridge, 9,700 ft. elev., October 17, 1940. F-416007

TALL-SHRUB COMMUNITIES

Four communities or groups of communities dominated by tall shrubs are included under this heading. These are shrub communities on south-facing, colluvial slopes, scattered tall shrubs on residual soils, shrubs growing in association with, and marginal to, spruce-fir timber, and a shrub-fringe community along streams and edges of wet meadows. The first three are dominated by species of Ribes, Symphoricarpos, Sambucus, or Prunus; the last by Salix. Examples of all but the second occur on the transect diagrammed in Fig. 2.

On steep, warm exposures, dense growths of *Symphoricarpos oreophilus*, *Ribes* spp., and *Prunus virginiana* occur, with an understory of many grasses and forbs. The composition of a stand of tall shrubs on a rocky, south-facing slope in Twelvemile Canyon (T19S, R3E, S13; elev. 9,500 ft.), varying from 30 to 50% in steepness, is given below, in the relative abundance (p. 92) indicated. Vegetation covers 52% of the surface, litter 6%, and bare ground and rock 42%.

Symphoricarpos oreophilus	3
Monardella odoratissima	3
Eriogonum neglectum	3
Aster chilensis	2
Sambucus racemosa	1
Castilleja viscida	1
Viguiera multiflora	1
Helianthella uniflora	1
Rosa fendleri	1
Achillea lanulosa	1
Orthocarpus tolmiei	1
Ribes inebrians	1
Stipa lettermani	1
Bromus carinatus	1
Agropyron trachycaulum	1
Polemonium foliosissimum	1
Lathyrus lanszwertii	1
Viola purpurea	x
Mahonia repens	x
Pachistima myrsinites	x
Stellaria jamesiana	x
Chenopodium album	x
Descurainia richardsonii	x
Penstemon subglaber	x
Frasera speciosa	x
Potentilla glandulosa	x
Gilia pulchella	x
Poa fendleriana	x
P. palustris	x
Ligusticum porteri	x
Agastache urticifolia	x
Taraxacum officinale	x
Vicia americana	x
Astragalus carltonii	x
Geranium richardsonii	x
Erigeron speciosus	x

There is a strong similarity between this list and that given as an example of the understory in the limber-pine community on another south exposure approximately 8 mi. away (p. 170). Over half the species recorded from the limber-pine understory are found in this tall-shrub stand, including *Symphoricarpos oreophilus*, *Monardella odoratissima*, *Castilleja viscida*, and *Ribes inebrians* as important species in both. Furthermore, *Mahonia repens* and *Pachistima myrsinites*, which were noted as forest indicators in the limber-pine understory, are also found here. Evidently, then, the two communities are related.

Landslips, which are common on these south-facing slopes, keep the soil in a perpetual state of immaturity (Figs. 5, 43). Nevertheless on many steep slopes the soil profile, although containing considerable rock, may be deep and distinct from the raw parent material (Fig. 44).

The vegetation of recent landslips is derived in part from roots, rhizomes, etc. already in the soil which are not too deeply buried, or too greatly exposed, to propagate. Rhizomatous species like *Aster chilensis* and *Aster glaucodes* persist in this fashion, and so do shrubs, especially *Ribes montigenum*, *Symphoricarpos oreophilus*, and *Rosa fendleri*. Of plants

FIG. 43. Landslips on a steep south exposure, North Fork of Manti Canyon. Sides of slip to left of center are fringed with tall shrubs, mostly *Prunus virginiana*. On toes of slips the chief shrub is *Symphoricarpos oreophilus*. *Ribes montigenum* and *R. leptanthum* are also common on this slope. Abundance of shrubs on slip margins is associated with concentrations of big rocks there; upper and central portions of slips are less rocky and support more forbs and grasses. 9,500 ft. elev. Sept. 18, 1948. F-464252

FIG. 44. Soil profile on steep south exposure under shrub cover of Prunus, Symphoricarpos, and Ribes. Note gravel in solum (above white string), here 90 cm deep. Colluvial character of parent material is evident. Slope measures 69%. Trail Ridge, 9,700 ft. elev. October 4, 1945. F-443876

that invade by seed, grasses are foremost. *Agropyron trachycaulum* and *Bromus carinatus* are more aggressive than other species. *Viguiera multiflora* often invades quickly, and to a lesser extent *Geranium richardsonii, Taraxacum officinale,* and *Agoseris pumila.* Species invading of course vary from place to place, depending on character of seed supply.

Accelerated erosion in the form of surface washing is common on these sites, but it is much less conspicuous than on slopes of lesser steepness under herbaceous vegetation. The reason for this is chiefly the density of the shrub cover and the litter layer beneath it. Livestock and game animals make trails along the slopes, more or less on the contour, and the displaced soil tends to be held fairly well by the securely rooted shrubs. Commonly where the soil is gashed by deep gullies like that permitting an exposure of the soil profile in Fig. 44, the cause is surface runoff from depleted herbaceous cover farther upslope.

A second type of tall-shrub community is found on the tops and shoulders of knolls and ridges, on residual rather than colluvial soils. The dominants are species of wild currant, mostly *Ribes inebrians* and to a lesser extent *R. montigenum.* The shrubs do not usually form a dense, exclusive cover but are intermingled with openings of upland-herb vegetation; and while they often occupy well-defined areas, they may also occur as isolated individuals in the grassland, forming a kind of savannah (Fig. 45). In places they are regularly spaced. These are the shrubs believed to be associated with the dark-spot patterns of aerial photos which turn out to be regularly spaced areas of deeper soil on knolls and ridges (p. 122).

Besides the two dominant currants, *Symphoricarpos oreophilus* and *Sambucus racemosa* sometimes form part of the overstory. The understory is essentially that of the surrounding upland-herb community. Because of accelerated erosion between the shrubs, intervening herbaceous vegetation may be

FIG. 45. Scattered *Ribes inebrians* on Wagon Road Ridge, 9,800 ft. elev., forming a kind of savannah. Living shoots of bushes are hedged back by sheep; general low vigor is indicated by volume of dead wood. Note pedestaling of grass tufts as an indication of current accelerated erosion. October 21, 1940. F-416017

reduced to that which occupies erosion-pavement areas. The protected soil beneath the shrubs, in contrast, commonly supports distinctly mesic plants. These are relatively palatable relics which provide clues to the original composition of the herbaceous cover. An example may be drawn from a stand of *Ribes montigenum* and *R. inebrians* near Swedish Knoll (T18S, R4E, S3; elev. 10,200 ft.). The slope, which faces south, is 30%. The shrubs form a complete cover over islands of uneroded soil alternating with relatively bare, rocky spaces, in which herbaceous cover varies from almost nothing to 20%. The last 8 species listed are found only in the shelter of currant bushes:

Artemisia discolor	*Lesquerella utahensis*
Stipa lettermani	*Pseudocymopterus montanus*
S. columbiana	
Bromus carinatus	*Festuca ovina*
Agropyron trachycaulum	*Thalictrum fendleri**
Aster chilensis	*Erigeron speciosus**
Achillea lanulosa	*Polemonium foliosissimum**
Taraxacum officinale	*Castilleja leonardi**
Potentilla pulcherrima	*Bromus anomalus**
Penstemon subglaber	*Rosa fendleri**
Symphoricarpos oreophilus	*Senecio uintahensis**
Vicia americana	*Poa palustris**

* Found only in protection of currant bushes.

Other common relics of the original herbaceous cover are *Aquilegia coerulea* and *Osmorhiza occidentalis.*

Ribes inebrians bushes often occur in the midst of patches of *R. montigenum,* suggesting invasion by *R. inebrians* and a successional relation. However, because young plants of *R. inebrians* are sometimes found growing in the open also, it is evident that the relation is not obligatory.

A description of what appears to be a soil formed in place under tall shrubs, as opposed to the colluvial soils of steep slopes, is given in Fig. 28, profile 952. The slope is 24% and the exposure southwest. A marked textural change, from 31 to 59% sand, occurs at 25 cm, but whether this indicates recent wind-deposition or a change in character of parent material is not clear. Organic-matter content and exchange capacity are high, but the most distinctive features of this profile are the relatively high pH values in the upper levels and the fact that shells of the burrowing snail, *Oreohelix strigosa depressa,* occur throughout the solum to a depth of 87 cm. Snail shells were also found at even greater depth in another shrub profile nearby.

A third tall-shrub community, much like the second but associated with conifers, and having *Ribes montigenum* almost invariably predominant, occurs in spruce-fir openings and as a fringe around practically every patch of spruce-fir timber. *R. inebrians* and *Sambucus racemosa* are often part of this community. These tall shrubs, particularly the spreading, thorny *R. montigenum,* may shelter mesic forbs like *Polemonium foliosissimum, Castilleja leonardi,* and *Mertensia leonardi* which invade the adjacent grassland only with some protection from grazing. Where an

area of spruce-fir forest has been logged or burned, these shrubs are dominant. Tree reproduction is virtually confined to the area covered by shrubs, and the invasion of these shrub-dominated areas by conifers makes a striking contrast with the lack of such invasion on adjacent areas of herbland. Evidently this tall-shrub community has an important place in the ecology of the conifer forest.

The fourth tall-shrub community, fringing streams and meadows, and dominated by willows, has been greatly modified and probably materially reduced in extent, by severe grazing and trampling. Reconstruction of its original cover, like that of the wet-meadow community with which it is associated, is not attempted here.

It cannot be said categorically that tall-shrub communities other than the willow fringe are characteristic of moist sites, in the same sense that wet-meadow communities are, and yet they do occur where soil moisture appears to be especially favorable. Tall shrubs, particularly *Ribes montigenum*, are abundant on northerly exposures in association with spruce and fir, and are succeeded by these trees. On southerly exposures they are associated with rocky soils (Fig. 5) or rock outcrops, as well as with fairly well stabilized talus. When they invade herbland it is beside logs that have been left lying during lumbering operations or where log fences have been built (Fig. 34), or on rocky sites from which soil has been stripped (Fig. 40). All such sites are believed to be moisture-conserving, where the balance is tipped in favor of woody species, either through reduced transpirational loss as on north exposures, through more available soil moisture per unit volume of root space as in rocky soils, or through lessened competition from herbaceous plants as along down logs.

SPRUCE-FIR ASSOCIATION

Although the spruce-fir association is the second largest community in the subalpine zone of the Wasatch Plateau, it has been little studied as yet and will receive brief treatment here. There are two reasons why this association has been neglected. One is that the spruce-fir understory is sparse and rather unimportant in point of volume of forage, as compared with the upland-herb association. The second is that few areas of coniferous forest are sources of accelerated runoff and erosion as compared with herbaceous communities. Mud-rock flows have come from forested areas after the cover has been burned off, but they have been much less frequent in historic times than mud-rock flows from herbaceous slopes denuded by overgrazing.

However the spruce-fir association is deserving of more study, both for scientific and economic reasons. One reason is to clarify its position in normal succession—either to prove or disprove, for one thing, the hypothesis set forth in this paper that spruce and fir, at least on warm, dry sites, are part of an early successional stage on talus leading to the upland-herb association. The origin of the small spruce-fir patches that occur here and there on fairly level ground is a related ecological problem that will perhaps provide an insight into climatic trends in the subalpine zone during the past several centuries. Many of these patches appear to have arisen on exactly the same kind of site as the surrounding herbland, but upon investigating, one finds a rockier, shallower soil than in the herbland (Fig. 17). On the economic side, the scanty spruce-fir understory, although not voluminous, appears to be important as summer forage for deer, and spruce and fir are an important local source of timber. Remote and formerly inaccessible stands are being cut today because of current high prices and the exhaustion of more accessible supplies. Efficient silviculture requires a more comprehensive knowledge of the ecology of these stands than we now possess.

SITE CHARACTERISTICS

The distribution of spruce-fir forests in relation to topography has already been described, and is illustrated in Figures 2, 3, and 4. The most extensive and densest spruce-fir stands are found on north exposures, and only small, scattered patches occur on level ground and south exposures. Characteristically evidences of seepage are associated with many of these patches, either as wet meadows or springs alongside the timber, or the patches of timber may be arranged along the contour of a headwater basin as if seepage from a particular stratum of level-lying limestone determined their occurrence (Fig. 46). It may be concluded, therefore, that soil moisture alone, or some combination of factors associated with soil moisture, limits the distribution of these conifers.

The spruce-fir soil profiles described in Table 5 were, with one exception, much shallower and contained much more skeletal material than nearby profiles under herbaceous vegetation. Another pair of profiles from the Block Mountain natural area are compared in Figure 47. The timber stand here is dominated by

FIG. 46. The contour arrangement of spruce-fir patches on this west-facing slope suggests a relation to seepage planes in the horizontal bedrock strata. Shrubs, mainly Ribes, dominate a large part of the slope. The lightest areas are herbland showing evidence of accelerated erosion. Straight Fork of Pleasant Creek, 10,000 ft. elev., Sec. 13, T15S, R5E, Aug. 18, 1949. F-464271

Engelmann spruce, with some codominant and many suppressed alpine firs. These trees are even-aged, between 80 and 90 years old. Scattered groups of larger spruce occur, 200 years old and older, relics of a fire that cleared the ground for the younger age class. Charred logs and charcoal in the soil attest the agency of fire. The forest profile is on a north exposure of 35% slope, the herbland profile on an east exposure of 48% slope. The two are within 100 yards of each other. Some gravel is found throughout the solum of each. A little charcoal is found throughout the solum of the forest profile, and some is found near the surface of the herbland profile.

SPRUCE-FIR	UPLAND-HERB
Duff +2 cm.	
Soil surface 0 cm.	Soil surface 0 cm.
Medium brown clay, breaking up into fine crumbs. Structure strongly influenced by fungal mycelia and roots, which give soil a porous, spongy character. −28 cm.	Dark brownish gray loamy clay; moderately compact; crumb structure; many fine roots. −25 cm.
Cloddy, compact light brown clay; nut structure; fewer roots. −52 cm.	Medium grayish brown clay; compact; nut structure; fewer roots. −85 cm.
Large limestone rocks with structureless tan clay between them.	Grayish brown clay; very compact; blocky structure with prismatic tendency; decomposing fragments of limestone. −105 cm.
	Structureless tan clay; limestone rocks.

FIG. 47. Comparison of two soil profiles, in spruce-fir forest and in upland-herb opening, Block Mountain natural area. (T20S, R4E, S9; elev. 10,000 ft.). Horizontal solid lines indicate soil surface and division between solum and parent material; broken lines indicate top of duff layer and minor zonal divisions.

Roughly, the solum under herbaceous vegetation is twice as deep as that under timber. It is also darker, at least below 24 cm, although a greater moisture content was partly responsible for this apparent difference. This difference in soil moisture is itself very striking and significant. The profiles were dug after a 2 weeks' rainy spell during which some 1.5 in. fell. (1.67 in. were recorded at the head of Ephraim Canyon, distributed among 12 out of 14 days.) The herbland profile was wet from the surface all the way down; the clay stuck to the shovel and had to be scraped off again and again. The forest profile, in contrast, was in no place more than moist, even at the surface, and its soil was crumbly, not sticky. The explanation appears to be that much of the rainfull was intercepted by the crowns, and much of that which reached the forest floor was retained by the duff, leaving little for the soil itself. Interception of summer rainfall by foliage and duff goes far to explain the sparsity of understory vegetation in these conifer stands.

A soil profile from near the head of Ephraim Canyon provides an example of a spruce-fir forest soil in somewhat greater detail (Fig. 28, profile 988). This profile was dug in a cut-over stand on a north exposure with 28 percent slope. It underlies a layer of duff 6 cm deep. The 7 cm layer below is a fairly clearly marked zone of transition, containing a high proportion of organic matter, between duff and mineral soil. Although the top of the C horizon is indicated at 51 cm, the zone above it is transitional, containing a large proportion of rock: the soil material analyzed in both horizons below 30 cm is in the nature of a matrix in which the rocks are embedded.

This soil is slightly more acidic near the surface than most of those described in Figures 9 and 28. Exchangeable hydrogen is correspondingly high. As in the soils of other types, exchange capacities are high throughout. The high proportion of sand in the C horizon, and correspondingly low proportion of silt, as compared with the overlying horizons, suggests that much of the sand in the solum has been weathered to silt.

VEGETATION

The shrubby and herbaceous understory in spruce-fir stands is very sparse, covering less than 5% of the surface. The soil is practically 100% covered by duff from conifer leaves and twigs.

Mosses are more abundant than in upland-herb communities, but they occur usually only in scattered patches. *Brachythecium collinum* (Schleich.) Br. & Sch. is the most common on all substrata. *Bryum* spp., *Mnium arizonicum* Amann, and *Timmia bavarica* Hessl. are often found on duff and rotten wood. *Dicranoweisia cirrhata* (L., Hedw.) Lindb. is very common in the crevices of logs. One stand of *Polytrichadelphus lyallii* Mitt. was found on the Wasatch Plateau on bared soil derived from sandstone. This was on Candland Mountain at an elevation of 10,000 ft. (T14-15S, R6E).

Two descriptions of specific stands will serve to characterize the understory vegetation of the spruce-fir community. Grazing by domestic livestock is probably not very influential in either instance, but grazing by deer may well be. The first example is from a north exposure on Block Mountain. The understory covers only 1 or 2% of the surface:

Ribes montigenum	4
Abies lasiocarpa	4
Aquilegia coerulea	2
Arnica cordifolia	2
Lonicera utahensis	x
Polemonium delicatum	x
Pachystima myrsinites	x
Osmorhiza obtusa	x
Viola canadensis	x
Sambucus racemosa	x
Lupinus alpestris	x

Aster engelmanni	x
Brachythecium collinum—duff and logs	
Bryum sp.—duff and logs	
Dicranoweisia cirrhata—logs	
Cladonia sp.—rotten logs	

The second example is from a spruce-fir stand about 150 years old on a north exposure at the head of Manti Canyon (north side of Elk Knoll). Understory cover is 20% or somewhat less:

Osmorhiza obtusa	4
Ribes montigenum	3
Abies lasiocarpa	2
Viola canadensis	2
Arnica cordifolia	2
Delphinium barbeyi	1
Epilobium angustifolium	1
Lupinus alpestris	1
Lonicera utahensis	x
Aquilegia coerulea	x
Geranium richardsonii	x
Thalictrum fendleri	x
Mitella stenopetala	x
Ligusticum porteri	x
Frasera speciosa	x
Brachythecium collinum—duff *Mnium arizonicum*—duff	1

Characteristic understory species of these timber stands are: *Osmorhiza obtusa, Arnica cordifolia, Viola canadensis,* and *Lonicera utahensis.* Occasionally one comes upon ericaceous plants—*Moneses uniflora, Pyrola secunda,* or *P. chlorantha* which suggest, like Polytrichadelphus, a more than commonly acidic substratum. These species are seldom found elsewhere.

Although the understory of spruce-fir forest is sparse, the herbaceous and shrubby vegetation around the margins of the timber, and in openings, is characteristically dense. *Ribes montigenum* commonly grows in a dense fringe around the edges of timber patches on dry sites, and on moist sites the tall-forb community may occur, dominated by *Delphinium barbeyi.* In general, the following species may be expected near the edges of timber, although some of them are unlikely to be in the open (e.g. *Mertensia, Erigeron, Castilleja* spp.) if grazing is severe:

Ribes montigenum	*Castilleja leonardi*
Sambucus racemosa	*C. miniata*
Mertensia leonardi	*Penstemon whippleanus*
Aster engelmanni	*Senecio crassulus*
Delphinium barbeyi	*Lathyrus lanszwertii*
Erigeron speciosus	*L. utahensis*
Lupinus alpestris	*Bromus carinatus*
Polemonium foliosissimum	*B. anomalus*
Geranium richardsonii	*Agropyron trachycaulum*
Thalictrum fendleri	*Carex festivella*

SUCCESSION

Spruce-fir forest is considered climax ,on steep, northerly exposures. On southerly exposures and on level ground and moderate slopes which are not subirrigated, however, spruce-fir forest appears to be a seral stage to a herbland climax. This hypothesis and the evidence upon which it is based have already been considered in detail (pp. 119, 122).

TALL-FORB COMMUNITY

Communities of very tall forbs, often forming dense stands as high as a man, are found in two kinds of sites in the subalpine zone. One is at the edge of wet meadows or beside springs of running water, usually adjacent to spruce-fir timber or patches of willows. The other is on areas in the lee of ridges where deep snowdrifts accumulate. Although its vegetation is commonly depleted, the soil of the former is often intact, while the soil of the latter, often stripped of all cover, is commonly greatly deteriorated from accelerated erosion. These tall-forb communities are seldom very extensive individually, but they occur frequently and in the aggregate provide a considerable volume of forage. They usually occur upon a very deep soil—a meter or more of solum is not uncommon.

Tall-forb communities on snowbank areas are especially liable to injury by grazing because they are usually on steep slopes, their growing season is short, they are attractive to grazing animals in midsummer when upland-herb vegetation is likely to be dry, and their wet soil is greatly compacted by trampling, giving rise to overland flow and accelerated erosion during late summer storms. As a result many of them are flood-source areas with an importance out of all proportion to their size (Fig. 48).

FIG. 48. "Snowbank area" on a steep east-facing slope where a snowdrift accumulates each winter. Remnants of *Delphinium barbeyi* indicate that this slope was formerly covered with a tall-forb community, and the depth and character of soil in places indicate that the original cover was luxuriant. The gullies, initially formed by occasional summer storms, are now kept open and enlarging by snowmelt every spring. Dark, slanting lines are sheep trails. Wagon Road Ridge, 10,000 ft. elev., October 21, 1940. F-416012

Delphinium barbeyi, the tall larkspur, is the most abundant and conspicuous species in the tall-forb community. It is also the most tenacious species where the soil is drastically eroded, often persisting on elevated hummocks of subsoil until these are at last destroyed and only erosion pavement remains. Quadrats 9 and 10, on an eroded snowdrift area at the head of Seely Creek, show *Delphinium barbeyi* to

have increased since 1913, and inspection of the slope as a whole suggests that the increase has been general there. It is probable that, if grazing and trampling were to be eliminated altogether, this species would continue to increase and would in time form a cover dense enough to prevent further erosion.

Delphinium barbeyi is a dominant among tall forbs on range that is lightly grazed or ungrazed by domestic livestock, but in such places other tall forbs are also conspicuous. A description of a tall-forb community at the head of Bear Creek (T18S, R4E, S1, elev. 10,000 ft.) follows:

Delphinium barbeyi	5
Aster foliaceus	1
Erigerón ursinus	1
Senecio crassulus	1
Mertensia leonardi	1
Poa reflexa	1
Artemisia discolor	1
Ligusticum porteri	x
Rumex mexicanus	x
Achillea lanulosa	x
Agropyron trachycaulum	x
Bromus carinatus	x
Hordeum nodosum	x
Chenopodium album	x
Descurainia richardsonii	x
Stellaria jamesiana	x
Erythronium grandiflorum	x
Geranium richardsonii	x
Polemonium foliosissimum	R
Osmorhiza occidentalis	R
Heracleum lanatum	R
Valeriana occidentalis	R

This stand is notable because of the persistence of Heracleum on range that is very heavily grazed. Heracleum is a rare plant in the subalpine zone, except in spots inaccessible, or almost inaccessible, to livestock. Polemonium, Osmorhiza, Valeriana, and Mertensia are also very palatable to sheep, and are all scarcer in this stand than they would be if it were less heavily grazed. The occurrence of the low-growing rhizomatous species, Erigeron, Artemisia, and Achillea, as well as the indicators of disturbance, Rumex and Chenopodium, reflects the periodic near-denudation and trampling the stand suffers.

There appears to be a close relation between the tall-forb and upland-herb communities because many of these tall, mesic forbs occur within natural areas and protected areas in upland-herb sites (Table 7), a fact that has been emphasized throughout this paper. Probably the distinction between upland-herb and tall-forb communities was not so clear-cut on the pristine range as it is today. Overgrazing and erosion have evidently eliminated whatever tall forbs may have been on the drier upland sites, and they have persisted only where livestock cannot get at them or, if grazed, where the soil-moisture content is high. Even here the proportion of choicer species has been reduced, with an attendant increase in *Delphinium barbeyi* and, because of denudation and erosion, more xeric forbs and grasses.

Wet-Meadow Communities

A number of streamside and meadow communities might be distinguished, one dominated by *Cardamine cordifolia*, one by *Caltha leptosepala*, another by *Pedicularis groenlandica*, still another by *Juncus balticus*, and so on. A sound subdivision of wet-meadow communities with proper evaluation of the effects of grazing, would require more detailed study than has been given, and probably a larger series of little-disturbed examples than can be found in the subalpine zone of the Wasatch Plateau today. Because they have been inadequately studied as yet, therefore, these various small communities are here grouped under one heading. All have sedges and one or the other species listed above as dominants, and often a fringe of willows and shrubby cinquefoil (*Potentilla fruiticosa*). For the most part these wet-meadow communities are small, seldom being larger than an acre. Many of them are simply narrow strips of mossy turf along streams overshadowed by willows. A few occur adjacent to small subalpine lakes.

The soil of the larger wet-meadow communities is usually deep. It has a high organic-matter content, but it is not an organic soil, in the sense of being derived from peat, as many mountain meadow soils are. Inorganic, rather than organic material, predominates in the profile. Wet-meadow soils, developing as most of them do in depressions, are a product in part of natural soil deposition from higher ground. To this natural process, deposition from accelerated erosion has been added, and parts of some meadows are covered with layers, not only of silt, but even of gravel and rock as a result of flooding from the slopes. This accumulation together with recent incision of the meadows themselves by gullies, places the normally high water table at a greater distance from the surface and results in the replacement of wet-meadow plants by less mesic species.

The only available description of a complete soil profile in a wet-meadow is given in Figure 28 (profile 999). During early summer the water table of this essentially level meadow is only a few cm from the surface; and as an indication of this fact the vegetation is predominantly *Caltha leptosepala*. The solum, which is overlain with a ½-cm layer of litter, is much darker than that of other soils, and is deeper than most. The proportion of organic matter in the uppermost 21 cm is higher, even, than in the forest profile. As in most other soils of the subalpine zone, exchange capacity is high, breaking off sharply between solum and parent material.

The five stands described in Table 30 give an idea of the variation in wet-meadow communities but they do not by any means embrace all the variations that occur. And yet it is clear that wet-meadow communities are poor in species as compared with the upland-herb association.

TABLE 30. Vegetal composition of 5 wet-meadow stands.* Abundance symbols are explained on page 92.

Stand number	953	966	963	967	968
Vegetation, percent	58	72	55	76	75
Litter, percent	12	10	38	23	9
Bare ground, percent	30	18	7	1	16
Grasses and sedges					
Agropyron trachycaulum	x†	..	x		
Carex festivella	1	1	1	1	1
C. hassei	..	x			
Eleocharis pauciflora	1	1	x	1	1
Hordeum nodosum	..	x	2	x	x
Juncus balticus	..	..	4	R	
J. castaneus	x				
Muhlenbergia richardsonis	x	3	..	..	x
Phleum alpinum	2	1	1	x	1
Poa reflexa	2	x	2	1	1
Trisetum spicatum	x	x	x	1	
Perennial forbs					
Achillea lanulosa	x	1	1	1	x
Angelica pinnata	..	..	..	x	x
Antennaria rosea	x†				
Aplopappus integrifolius	x	..	x	..	x
Aster foliaceus	..	..	x	..	x
Caltha leptosepala	2	4	x	4	5
Cardamine cordifolia	..	..	..	x‡	
Castilleja sulphurea	..	..	x		
Delphinium barbeyi	..	..	R		
D. nelsonii	..	x	..	..	x
Dodecatheon alpinum	2	1	x	1	1
Epilobium hornemanii	1	2	x	1	2
Erigeron ursinus	1†	1	3†	3	1
Habenaria sp.	..	R			
Lathyrus lanszwertii	x†				
Ligusticum porteri	..	x			
Pedicularis groenlandica	..	..	..	1	1
Plantago tweedyi	2	1	2	1	1
Potentilla pulcherrima	2	..	x		
Rumex mexicanus	..	..	x	x	
Saxifraga arguta	..	..	..	x‡	
Senecio crassulus	..	x	x	..	x
Stellaria umbellata	..	x	..	x	
Taraxacum officinale	1	1	1	1	1
Valeriana edulis	..	..	..	x	x
Veronica americana	..	..	..	..	x
Vicia americana	..	x			
Zigadenus elegans	2	3	x	2	1
Annuals					
Androsace septentrionalis	x				
Descurainia richardsonii	..	..	..	..	x
Draba stenoloba	..	..	..	x	
Mosses	4	3	3	3	3

*Stand 953. Horseshoe Flat, T17S, R4E, S14, 10,000 ft. elev.
Stand 966. Horseshoe Flat, T17S, R4E, S12, 10,000 ft. elev.
Stand 963. Horseshoe Flat, T17S, R4E, S14, 10,000 ft. elev.
Stand 967. Near Snow Lake, T18S, R4E, S15, 10,000 ft. elev.
Stand 968. Head Lowry Fork, T18S, R4E, S16, 10,000 ft. elev.

†Occurring chiefly in driest parts of stand.

‡Evidently a relic; found only in spots sheltered from sheep.

All five stands are characterized by a high degree of cover and a turf of mosses, chiefly species of *Bryum* and *Brachythecium*. The constant species, *Carex festivella, Eleocharis pauciflora, Phleum alpinum, Poa reflexa, Caltha leptosepala, Dodecatheon alpinum, Erigeron ursinus, Plantago tweedyi, Zigadenus elegans,* and *Epilobium hornemanii,* besides the more xeric *Achillea lanulosa* and *Taraxacum officinale,* are evidently species that are particularly resistant to grazing, for they are found in nearly all meadows, frequently persisting as remnants in former meadows now being desiccated by gully drainage. The scarcity of *Angelica pinnata, Cardamine cordifolia,* and *Saxifraga arguta* is probably referable in part to their elimination by heavy grazing.

Many heavily grazed depressions that are periodically flooded support almost pure stands of *Hordeum nodosum,* and those in which sediment deposition is rapid and the water level recedes leaving a bare expanse, may be covered with *Rumex mexicanus* or *Oenothera flava* to the exclusion of other species. It seems clear that such pure stands are temporary disturbance communities.

Some meadows occur in the subalpine zone which appear to be less heavily grazed than the stands in Table 30, with an even heavier, more continuous turf containing a species of *Mnium,* and having dwarf and shrub willows as prominent constituents of the cover. From the eagerness with which willows are browsed, especially by sheep, it is probable that they have been greatly reduced in practically all meadows. Those that survive, like *Salix scouleriana,* are tall enough to grow beyond the reach of the animals; dwarf willows are practically extinct.

Figure 49 shows the meadow vegetation fringing a small lake where livestock have been unable to graze and illustrates a segment of normal hydrarch succession. The fringe itself consists of a moss layer (*Bryum* sp.) and:

FIG. 49. The margin of a shallow lake where grazing by livestock does not occur. The lake is filling in with sediment and logs. A zone of sedge is succeeded by a zone of willow and spruce. Spruce in center is 46 cm tall. Current growth of willows has been browsed by deer. Head of Twelvemile Canyon (T19S, R4E, S19, 10,000 ft. elev.). August 14, 1947. F-464230

Carex festivella	*Epilobium hornemanii*
Juncus tracyi	*Cardamine cordifolia*
Deschampsia caespitosa	*Mimulus guttatus*
Veronica americana	*Saxifraga arguta*

Above this fringe on drier ground occurs a community transitional to either the upland-herb or spruce-fir association:

Salix glaucops	*Angelica pinnata*
Lonicera involucrata	*Geranium richardsonii*
Solidago ciliosa	*Mertensia leonardi*
Lupinus alpestris	*Picea engelmanni*
Taraxacum officinale	

Alpine Relic Community

A singular group of plants, found only in a very few places in the subalpine zone, is worthy of note. These plants are:

Primula parryi	*Ranunculus adoneus*
Synthyris laciniata	*Anemone globosa*
Ivesia gordonii	

This community is found on steep, rocky exposures, usually where the snow hangs late. It happens to occur in places so steep and rugged as not to be disturbed by livestock. The substratum in which the plants are rooted has undergone very little change beyond weathering of the parent shale and limestone. It contains essentially no organic matter, and can hardly be termed a soil.

A good example of this community occurs at the head of Canal Canyon, where Primula is abundant (T16S, R5E, S31, 10,300 ft. elev.). This is the cirque of a Pleistocene valley glacier (Spieker & Billings 1940). Ivesia has been found in one other locality, on Wasatch Peak (T19S, R4E, S34, 10,000 ft. elev.). The spread of this species into Horseshoe Flat, in association with rock exposure by accelerated erosion, has already been described (p. 165). Synthyris and Ranunculus are more widespread, occurring in cool rocky sites, and Anemone is even more widely distributed, on erosion pavement areas.

SUMMARY AND CONCLUSIONS

The purposes of this study are to reconstruct the character of original vegetation in the subalpine zone of the Wasatch Plateau in central Utah, which has been greatly modified since settlement, and to describe the changes it has undergone as a result of grazing by livestock. Most attention is given the herbaceous vegetation of dry and mesic sites. To understand this vegetation it has been necessary to work out the salient characteristics of soil development and primary succession.

Characteristics of Subalpine Zone

The subalpine zone includes the highest parts of the plateau, with an average elevation of about 10,000 ft. The axis of the plateau (an erosional remnant of a vast uplift that extended eastward into Colorado), lies approximately north and south, like a backbone, and has riblike ridges extending at right angles from it. Its topography, developed from horizontal Cretaceous and Tertiary strata, is prevailingly rolling, but the edges of the ridges are in many places abrupt cliffs. Slumping is common.

Climate of the subalpine zone is humid compared with that of the inhabited lowlands. Annual precipitation is in excess of 30 in. About two-thirds falls between November 1 and May 1, mostly as snow, and a deep snow mantle accumulates until early in May. Melting is usually over, except for deep snowdrifts, between the first and middle of June. This winter precipitation is the principal source of yearlong stream flow. It causes high water in spring, but not destructive floods like those produced by summer storms, and it has caused little of the accelerated erosion now prevalent in the subalpine zone. The remaining third of the annual precipitation falls mostly as rain, and in July, August, and September may occur in torrential storms, causing very rapid soil erosion where vegetal cover has been materially reduced, and giving rise to floods of the mud-rock flow type.

Temperatures are generally low and moderate, maxima seldom exceeding 70° F in summer, and minima in winter seldom being much lower than those in Sanpete Valley, to the west of the plateau. Freezing temperatures occasionally occur in summer, but not often. A deep snow blanket insulates the soil in winter, so that frost-heaving does not occur during periods of prolonged, intense cold.

Winds are prevailingly from the west. Average daily wind movement well above the ground is on the order of 175 mi.; close to the surface it is on the order of 65 mi. There appears to be little seasonal variation in wind movement. Evaporation in the open grassland is rapid, being on the order of evaporation in other open alpine and subalpine sites in the Rocky Mountains.

Soils are heavy, mostly clays and clay loams, and moisture equivalents of surficial samples average about 33%. Soil acidity ranges closely about pH 6.3, and normal organic-matter content is about 8% for herbland soils and higher for forest and shrubland soils. The soil is saturated with moisture during the snowmelt period each spring. Its measured moisture content trends from about 40% in early spring to about 15% in late fall, varying greatly with amount and frequency of summer precipitation. While moisture content of the uppermost 6 in. frequently drops below the wilting coefficient, that of the 12-18 in. depth seldom drops so low, and then very late in summer. The upland-herb soil profile is usually on the order of half a meter in depth, and when well developed is virtually free of rocks except occasional fragments of cherty limestone. It grades from granular structure at the surface, through nutty, to a structure that is weakly prismatic. There is an abrupt change in color, structure, and rock content between the solum proper and weathered parent material below it, but there is little evidence of zonation within the solum. Only as the parent material is approached does a carbonate reaction become manifest. Annual percolation of a great volume of snowmelt evidently has a profound influence on soil development.

The original large animals were almost entirely destroyed before the turn of the century. Elk, which have been introduced, and mule deer, have increased very greatly in recent years, and mule deer, at least,

are now overabundant in some parts of the plateau. Predators—coyotes, cougar, bear—are relentlessly hunted. Small mammals, particularly pocket gophers, evidently have a material influence upon vegetation and soil of the subalpine zone, but as yet only a little specific study of their influence has been made.

The dominant influence of animals has been the grazing of domestic livestock, beginning in the subalpine zone about 1870. Quick profits in exploitative use of this virgin grazing land drew transient herds from Colorado and Oregon, as well as local herds, and the plateau was so overrun with sheep that it became reduced, in the '80's and '90's to "a vast dust bed," the source of torrential floods and polluted stream flow. These abuses of the watershed through unregulated grazing led to the creation in 1903 of what is now the Manti National Forest. The abolition of transient herds and regulation in period and amount of grazing was probably a more profound change than any that has occurred since, although improvements in management, including reductions in stocking on the order of 25%, have been made over the past 40 years. Much of the subalpine zone was so greatly deteriorated at the time the Forest was created, however, that management and reductions so far imposed have been insufficient to halt continuing attrition of the soil.

Plant Communities

The occurrence and extent of the major plant communities in the subalpine zone are determined principally by topographic factors and the local climates associated with them. Soil parent material is evidently of minor importance.

The most important community is the mixed upland-herb association. It occurs on level areas or moderate slopes, and where it has not been greatly disturbed and eroded its soil is usually deep and rock-free. The importance of this association derives from the fact that it is extensive, that it is considered particularly desirable for forage, and that it is more vulnerable than any other to denudation by overgrazing. Most of the accelerated erosion observed today in the subalpine zone occurs in variants of the mixed upland-herb association, and it is the chief source of torrential summer floods. Between grazing and watershed values, therefore, this association has become the focus of a conflict in use. The bulk of this paper is devoted to this association and the variations of it that have brought about by overgrazing. These variations, which will be summarized subsequently, are grouped as follows.

1. Forb-dominated communties on cattle range
2. Grass-dominated communities on sheep range
3. Low-shrub communities
4 Communities of ephemeral species
5. Erosion-pavement communities

The community second largest in areal extent in the subalpine zone is the spruce-fir association, of small value for grazing by domestic livestock, but important as cover for game and as timber. The dominants are Engelmann spruce and alpine fir. Understory vegetation is usually sparse, a fact largely attributable to interception of summer rainfall by the trees. In sizable openings, however, tall herbaceous vegetation grows luxuriantly. These spruce-fir forests occupy north exposures, especially where slopes are steep, and occur as small, scattered patches in the open upland-herb association. The occurrence of the forests seems to depend primarily upon a slightly greater-than-average moisture balance. The spruce-fir association is considered to be climax upon northerly exposures and in moist spots, and a seral stage on talus slopes of southerly exposure, where it is succeeded by tall shrubs and ultimately the upland-herb association. Spruce and fir show no evidence of succeeding the upland-herb association.

A tree-dominated community of much smaller extent is characterized by limber pine. Sometimes in association with Douglas-fir, Engelmann spruce, or alpine fir, limber pine occupies the shoulders of ridges and steep southerly exposures, anchored in rock crevices. The trees are scattered, not forming a closed canopy. Understory vegetation is sparse because of the outcropping of ledges and natural instability of loose soil materials. The shrubs, forbs, and grasses are those of tall-shrub communities of similar sites. The limber pine community is obviously dependent for its perpetuation upon the existence of escarpments. When the slopes are reduced to talus, spruce and fir as well as tall shrubs, become dominant, and as greater and greater stability is achieved, and a deeper and more continuous soil mantle is developed, these give way to herbaceous cover.

The principal tall-shrub communities are dominated by species of *Ribes*, *Symphoricarpos*, *Sambucus*, and *Prunus*. They include extensive stands on steep, south-facing slopes with rocky soils. Frequent landslides keep these soils immature, but when the slopes are reduced in steepness and greater stability is achieved, herbaceous cover evidently replaces the shrubs. A second tall-shrub community occurs as scattered bushes on residual soils on the tops of ridges, and evidently this is also replaced by forbs and grasses in time. A third tall-shrub community occurs in association with spruce-fir timber, and a fourth, dominated by willows, is marginal to meadows and streams. In general, tall-shrub communities occupy sites which have—either because of rocky soil, northerly exposure, or a high water table—greater moisture-conserving properties than sites occupied by upland-herb vegetation.

All wet-meadow communities are here grouped into one, although it is recognized that several might be distinguished. The wet-meadow communities on the Wasatch Plateau are so few and small, and have been so greatly affected by grazing, accelerated erosion, and accelerated deposition, that they do not permit a very adequate appraisal of the hydrosere.

An alpine relic community is recognized on certain steep northerly exposures where snow hangs late.

These stands which are few and small, are probably relics of Pleistocene glaciation.

The tall-forb community usually dominated by *Delphinium barbeyi*, is found in certain "snowbank areas" and on cool, moist slopes near the edges of spruce-fir forest. These stands are never extensive, but they support a volume of forage out of proportion to their area. They are of particular significance because their soils are especially liable to puddling and compaction as a result of overgrazing, easily giving rise to floods. It appears that several mesic species now occurring almost entirely in the tall-forb community were formerly abundant and widespread in the upland-herb association, and it may well be that the distinction between the two communities has been artificially heightened as a result of overgrazing.

To summarize primary successional relations: On cool, moist slopes of limestone talus, scattered trees of spruce and fir are pioneers. The climax community is a closed forest of spruce and fir. The alpine relic community may give way to spruce and fir when the substratum is stable enough to support trees, and it is probable that there are successional interrelations in the hydrosere between wet-meadow communities, the spruce-fir association, and the upland-herb association, but these have not yet been worked out.

On talus slopes of warm, dry exposures, spruce and fir invade deep crevices as pioneers. A few tall shrubs and some forbs and grasses may also occur in such crevices, but spruce and fir are most conspicuous. The influence of lichens and mosses in disintegration of the limestone appears to be slight, as compared with direct atmospheric weathering. In gravelly pockets a number of grasses and low forbs are pioneers. As the rocks disintegrate and spaces between them become filled with soil, trees and shrubs become denser, with an understory of tall forbs and grasses characteristic of the herbaceous climax. Eventually, with more complete disintegration of the rock, deepening of the soil, and occupance of the soil mass by the fine roots of herbaceous species, woody plants fail to be replaced, and a mixed forb-grass climax results. The transition may be directly from mixed trees and shrubs to herbland or by way of an intermediate stage in which few trees are present and shrubs are dominant. There is also evidence of succession on residual soils from a shrub savannah to the mixed upland-herb association.

Mixed Upland-Herb Association

Natural areas, relic forbs and grasses in the shelter of shrubs, observation of range under different degrees of use, and trends in secondary succession following the elimination of grazing, all indicate an original vegetation of more mesic character than prevails today. Rather than a single dominant species over any extensive area, the original upland-herb association appears to have been a mixture of many species of tall, rather succulent forbs, grasses, and sedges. The following species were probably among the most prominent:

Mertensia leonardi	*Bromus carinatus*
Agropyron trachycaulum	*B. anomalus*
Valeriana occidentalis	*Carex festivella*
Osmorhiza occidentalis	*C. hoodii*
Heracleum lanatum	*C. raynoldsii*
Angelica pinnata	*Aquilegia coerulea*
Polemonium foliosissimum	*Castelleja sulphurea*
Erigeron speciosus	*C. leonardi*

The cover of vegetation and litter (as measured with the point analyzer) was undoubtedly well in excess of 50% on most situations with a well-developed soil mantle, and probably was of the order of 70%. Within a given stand vegetation and litter were uniformly dispersed, with bare spaces small and scattered, in contrast to patchy vegetation with bare, eroding soil between patches that occurs in many places today. Observable erosion of the surface soil was absent throughout practically the entire community.

A summary of the effects of grazing on secondary succession and on soil erosion is given in the section "Discussion: the Influence of Grazing," page 166.

When the original mixed upland-herb vegetation was destroyed, by a degree of overgrazing and trampling almost inconceivably severe, the surface soil was eroded in many places, and the water table was lowered by dissection of the soil mantle with gullies. Communities of ephemeral species dominated by annual weeds (e.g., *Chenopodium album, Polygonum douglasii, Descurainia richardsonii*) and early withering perennials (e.g., *Viola nuttallii, Stellaria jamesiana, Claytonia lanceolata*) succeeded. In certain extensive areas, these have been superseded in dominance by *Madia glomerata*, spreading from sheep bedgrounds. These various ephemeral communities rarely provided effective soil protection, and then only during brief periods of maximum growth. During most summers the soil under them was readily eroded by torrential storms.

Accelerated erosion has removed varying amounts of topsoil, and organic-matter content varies today from about 8% near the surface of uneroded soils to less than 2% in severely eroded soils. These severely eroded soils are essentially subsoils and have a harsh surface so that reestablishment of vegetation on them is made difficult if not impossible.

Where erosion was particularly rapid, or where the soil was naturally shallow, "erosion pavement" has been formed—fragments of chert and limestone have accumulated at the surface after the fine particles were washed or blown away. The vegetation of these pavement areas is much like that on pockets of shallow, gravelly soil in early stages of primary succession. In some places *Ivesia gordonii*, normally a crevice plant in alpine situations, has spread following loss of the soil mantle. Except for exposed bedrock, which is much less common than erosion pavement, erosion-pavement areas represent the most extreme deterioration in the subalpine zone. Con-

tinued grazing and trampling by livestock keep them from becoming stabilized; indeed, it is by no means certain that they can become stabilized in a reasonable time without artificial restorative measures in addition to the exclusion of livestock.

On sites where the original soil mantle was deeper or the natural erosion potential less, and following improvements in grazing management, communities of ephemeral species have been invaded by perennials. On sheep range the invading species have been preponderantly grasses (*Stipa lettermani, Agropyron trachycaulum, Trisetum spicatum, Bromus carinatus*), although *Taraxacum officinale* and the rhizomatous forbs *Achillea lanulosa, Artemisia discolor,* and perhaps *Penstemon rydbergii,* have also invaded strongly. On cattle range grasses have generally been suppressed, and the chief invaders have been *Geranium richardsonii,* Taraxacum, and the rhizomatous species, Artemisia, Penstemon, *Aster chilensis,* and *Erigeron ursinus.* These trends are related to the respective forage preferences of sheep and cattle, as well as to the phenological and morphological characteristics of the plants.

Three species of low shrubs have also invaded these uplands aggressively since grazing by domestic livestock began. These are *Chrysothamnus viscidiflorus, Artemisia rothrockii,* and (at the northern, lower end of the plateau), *A. tridentata.* The first two, at least, dominate areas on which herbaceous vegetation was probably very severely depleted years ago. These low shrubs are not likely to be superseded by herbaceous vegetation in the near future, even if all grazing were to be excluded, for they are long-lived.

When intensity of grazing is lessened, tall, mesic forbs (and certain grasses and sedges) tend to increase in grass-dominated communities on sheep range, and tall, mesic grasses and sedges (and certain forbs) tend to increase in forb-dominated communities on cattle range, a trend toward restoration of the original, mixed upland-herb vegetation. The restoration cannot be complete during the lifetime of any persons now living, however, because of the soil losses that have occurred and that are still occurring. Nor will the original vegetation ever be precisely restored, because of the probable persistence of introduced species. It is possible, too, that certain species present in the original vegetation have been completely exterminated in the subalpine zone of the Wasatch Plateau.

Among species that records show to have increased markedly in the subalpine zone since domestic livestock began to graze the plateau, and that still appear to be increasing are:

Taraxacum officinale	*Artemisia discolor*
Chrysothamnus viscidiflorus	*Helenium hoopesii*
Artemisia rothrockii	*Madia glomerata*
A. tridentata	*Penstemon rydbergii*

Some of these species have been introduced to the subalpine zone since the white man's occupation of Utah. Annual weeds, *Polygonum douglasii, Chenopodium album, Descurainia richardsonii, Lepidium densiflorum, et al.* (species also probably introduced) were very abundant until about 1920. Since then they have diminished generally, tending to be replaced either by another introduced annual, *Madia glomerata,* or by perennial forbs and grasses. The rhizomatous forb, *Achillea lanulosa,* reached a peak in dominance about 1920, and has since diminished greatly in dominance throughout most of the subalpine zone, whereas other rhizomatous species (*Artemisia discolor, Penstemon rydbergii*) which have been increasing steadily for many years, tend to maintain their dominance, especially under heavy grazing. These and other rhizomatous forbs facilitate the invasion of grasses and forbs that reproduce only by seed, evidently by modifying microclimate and stabilizing soil of formerly denuded surfaces.

The concept of secondary succession developed in this study includes three successional levels. At the top is the upland-herb community, varying in composition from place to place but having tall, mesic forbs, grasses, and sedges as dominants. At the bottom are communities of low-growing ephemeral species, annuals and perennials that usually wither and leave the ground bare before summer is over. In an intermediate position lie grass-dominated communities of sheep range, low-shrub communities, and forb-dominated communities of cattle range. These communities, which predominate in the subalpine zone today, have the common characteristic of being more xerophytic than the original mixed upland-herb association. They are not related successionally to one another, but are of essentially equivalent rank. While the successional relations described in this study agree in some details with those presented in an earlier study by Sampson (1919), they differ in many important respects. The chief differences relate to the concept of climax, the relation between primary succession and secondary succession due to overgrazing, and the relation between certain stages in secondary succession.

Very great increases in vegetation have occurred in many parts of the subalpine zone during the last 40 years, but changes in vegetation on permanent quadrats during the past decade or two suggest that this upward trend has ceased. It appears, therefore, that management practices which succeed in raising the range from the lowest stage in secondary succession may still not be adequate for continuing improvement.

The fact is also clearly evident that losses of soil by accelerated erosion are continuing. Once well under way, accelerated erosion acquires a momentum that is increasingly difficult for vegetation to stop unaided. Stabilization of many slopes that have been eroding for years appears impossible, before all soil is lost, without artificial help. In considering changes in vegetation and soil the process of accelerated erosion must be recognized as something distinct from succession. Accelerated soil erosion is not a successional process, the converse of soil develop-

ment; it is simply soil destruction. When all the soil mantle has been stripped away, leaving only bed-rock or erosion pavement, rapid improvement through secondary succession is no longer possible: the only possibility of improvement is by the painfully slow process of soil formation and primary succession.

LIST OF SEED PLANTS

PINACEAE

Abies lasiocarpa (Hook.) Nutt.
Juniperus communis L.
Picea engelmanni Parry
Pinus flexilis James
Pseudotsuga taxifolia (Poir.) Britton

GRAMINEAE

Agroypron dasystachyum (Hook.) Scribn.
Agropyron riparium Scribn. & Smith
Agropyron subsecundum (Link) Hitchc.
Agropyron trachycaulum (Link) Malte
Bromus anomalus Rupr.
Bromus carinatus Hook. & Arn.
Bromus inermis Leyss.
Calamagrostis scopulorum Jones
Deschampsia caespitosa (L.) Beauv.
Elymus salina Jones
Festuca ovina brachyphylla (Schult.) Piper
Hesperochloa kingii Rydb.
Hordeum nodosum L.
Melica bulbosa Geyer
Muhlenbergia richardsonis (Trin.) Rydb.
Phleum alpinum L.
Phleum pratense L.
Poa fendleriana (Steud.) Vasey
Poa interior Rydb.
Poa nevadensis Vasey
Poa palustris L.
Poa pratensis L.
Poa reflexa Vasey & Scribn.
Sitanion hystrix (Nutt.) J. G. Smith
Stipa columbiana Macoun
Stipa lettermani Vasey
Trisetum spicatum (L.) Richt.

CYPERACEAE

Carex eleocharis Bailey
Carex festivella Mkze.
Carex hassei Bailey
Carex haydeniana Olney
Carex hoodii Boott
Carex raynoldsii Dewey
Eleocharis pauciflora (Lightf.) Link

JUNCACEAE

Juncus balticus montanus (Willd.) Engelm.
Juncus castaneus J. E. Smith
Juncus saximontanus A. Nels.
Juncus tracyi Rydb.

LILIACEAE

Erythronium grandiflorum Pursh
Smilacina stellata (L.) Desf.
Zigadenus elegans Pursh

SALICACEAE

Populus tremuloides Michx.
Salix glaucops Anders.
Salix scouleriana Barr.

POLYGONACEAE

Eriogonum neglectum Greene
Polygonum douglasii Greene
Polygonum kelloggii Greene
Rumex mexicanus Meisn.

CHENOPODIACEAE

Chenopodium album L.
Monolepis nuttalliana (Schult.) Greene

PORTULACACEAE

Claytonia lanceolata Pursh

CARYOPHYLLACEAE

Arenaria nuttallii Pax.
Silene lyallii S. Wats.
Silene petersonii Maguire
Stellaria jamesiana Torr.
Stellaria umbellata Turcz.

RANUNCULACEAE

Anemone globosa Nutt.
Aquilegia coerulea albiflora Gray
Caltha leptosepala DC.
Clematis hirsutissima Pursh
Delphinium barbeyi Huth
Delphinium nelsonii Greene
Ranunculus adoneus Gray
Ranunculus inamoenus Greene
Thalictrum fendleri Engelm.

BERBERIDACEAE

Mahonia repens (Lindl.) G. Don.

CRUCIFERAE

Arabis lyallii S. Wats.
Cardamine cordifolia Gray
Descurainia richardsonii incisa (Engelm.) Detling
Draba stenoloba nana (Schulz.) C. L. Hitchc.
Erysimum elatum Nutt.
Lepidium densiflorum Schrad.
Lesquerella utahensis Rydb.
Thlaspi glaucum A. Nels.

CRASSULACEAE

Sedum stenopetalum Pursh

SAXIFRAGACEAE

Mitella stenopetala Piper
Ribes inebrians Lindl.
Ribes leptanthum Gray
Ribes montigenum McClatchie
Saxifraga arguta D. Don.

ROSACEAE

Fragaria bracteata Heller
Holodiscus discolor (Pursh) Maxim.
Ivesia gordonii (Hook.) Torr. & Gray
Potentilla fruticosa L.
Potentilla glandulosa Lindl.
Potentilla pulcherrima Lehm.
Prunus virginiana melanocarpa (A. Nels.) Sarg.
Rosa fendleri Crépin
Rubus idaeus L.

LEGUMINOSAE

Astragalus carltonii Macbr.
Astragalus goniatus Nutt.
Lathyrus lanszwertii Kellogg
Lathyrus utahensis Jones
Lupinus alpestris A. Nels.
Lupinus foliosus Nutt.
Vicia americana Muhl.

GERANIACEAE

Geranium richardsonii Fisch. & Trautv.

LINACEAE

Linum lewisii Pursh

CELASTRACEAE

Pachistima myrsinites (Pursh) Raf.

VIOLACEAE

Viola adunca J. E. Smith
Viola canadensis L.
Viola nuttallii linguaefolia (Nutt.) Jepson
Viola purpurea Kellogg

ONAGRACEAE

Epilobium angustifolium L.
Epilobium hornemanii Reichenb.
Gayophytum ramosissimum Torr. & Gray
Oenothera flava (A. Nels.) Munz

UMBELLIFERAE

Angelica pinnata S. Wats.
Heracleum lanatum Michx.
Ligusticum porteri Coult. & Rose
Lomatium nuttallii (A. Gray) Macbr.
Orogenia linearifolia S. Wats.
Osmorhiza obtusa (Coult. & Rose) Fernald
Osmorhiza occidentalis Nutt.
Pseudocymopterus montanus (Gray) Coult. & Rose

ERICACEAE

Moneses uniflora (L.) Gray
Pyrola chlorantha Swartz.
Pyrola secunda L.

PRIMULACEAE

Androsace septentrionalis puberulenta (Rydb.) Knuth
Dodecatheon alpinum (Gray) Greene
Primula parryi Gray

GENTIANACEAE

Frasera speciosa Dougl.
Gentiana heterosepala Engelm.

POLEMONIACEAE

Collomia linearis Nutt.
Gilia pulchella Dougl.
Polemonium delicatum Rydb.
Polemonium foliosissimum archibaldae (Nels.) Wherry

HYDROPHYLLACEAE

Phacelia heterophylla Pursh
Phacelia sericea (Graham) Gray

BORAGINACEAE

Mertensia leonardi Rydb.

LABIATAE

Agastache urticifolia (Benth.) Kuntze
Monardella odoratissima Benth.

SCROPHULARIACEAE

Castilleja leonardi Rydb.
Castilleja miniata Dougl.
Castilleja sulphurea Rydb.
Castilleja viscida Rydb.
Mimulus guttatus DC.
Orthocarpus tolmiei Hook. & Arn.
Pedicularis groenlandica Retz.
Penstemon cyananthus Hook.
Penstemon rydbergii A. Nels.
Penstemon subglaber Rydb.
Penstemon whippleanus Gray
Synthyris laciniata (Gray) Rydb.
Veronica americana Schwein.

PLANTAGINACEAE

Plantago tweedyi Gray

RUBIACEAE

Galium bifolium S. Wats.
Galium boreale L.

CAPRIFOLIACEAE

Lonicera involucrata Banks
Lonicera utahensis S. Wats.
Sambucus racemosa L.
Symphoricarpos oreophilus Gray

VALERIANACEAE

Valeriana edulis Nutt.
Valeriana occidentalis Heller

COMPOSITAE

Achillea lanulosa Nutt.
Actinea acaulis arizonica (Greene) Blake
Agoseris arizonica Greene
Agoseris pumila (Nutt.) Rydb.
Agoseris taraxacifolia (Nutt.) D. Dietr.
Antennaria arida E. Nels.
Antennaria rosea Greene
Aplopappus integrifolius Porter
Aplopappus macronema Gray
Aplopappus parryi A. Gray
Arnica arcana A. Nels.
Arnica cordifolia Hook.
Artemisia discolor Dougl.
Artemisia frigida Willd.
Artemisia rothrockii Gray
Artemisia tridentata Nutt.
Aster chilensis adscendens (Nees) Lindl.
Aster engelmanni (D. C. Eaton) Gray
Aster foliaceus canbyi (Lindl.) Gray
Aster glaucodes Blake
Chaenactis douglasii (Hook.) Hook. & Arn.
Chrysothamnus viscidiflorus lanceolatus Hall & Clements
Chrysothamnus nauseosus (Pall.) Britt.
Cirsium drummondii Torr. & Gray
Crepis acuminata Nutt.
Erigeron compositus glabratus (Pursh) Macoun
Erigeron speciosus macranthus (Lindl.) Nutt.
Erigeron ursinus D. C. Eaton
Helenium hoopesii Gray
Helianthella uniflora (Nutt.) Torr. & Gray
Madia glomerata Hook.
Rudbeckia occidentalis Nutt.
Senecio ambrosioides Rydb.
Senecio amplectens Gray
Senecio crassulus Gray
Senecio cymbalarioides Nutt.
Senecio fendleri Gray
Senecio mcdougalii Heller
Senecio multilobatus T. & G.
Senecio uintahensis (A. Nels.) Greenm.
Solidago ciliosa Greene
Solidago parryi (Gray) Greene
Taraxacum officinale Weber
Townsendia montana Jones
Viguiera multiflora (Nutt.) Blake

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ECOLOGICAL RELATIONS OF THE BREEDING BIRD POPULATION OF THE DESERT BIOME IN ARIZONA

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INTRODUCTION

Bird populations of the lower Sonoran deserts have been long neglected, due primarily to the hardships encountered and the inaccessibility of most areas that are relatively undamaged by human intervention. Few areas remain with unspoiled desert flora and fauna so characteristic of the "old southwest." In this hard climate, overgrazing, overshooting, fires, and other catastrophes leave scars for long periods of time. Recovery is slow, because there is little rainfall to invigorate plant successions. Accessible bodies of permanent natural water are usually surrounded by extensive, barren areas due to trampling by cattle.

The Organ Pipe Cactus National Monument, Pima County, Arizona, was selected as the site for the present study. It contains 330,687 ac. or 516 sq. mi. of luxuriant growth. About one thousand head of cattle inhabit the area, but only in the vicinity of water holes is their presence noticeable to any extent. The Monument is situated 15 miles south of Ajo, Arizona, and is crossed by an improved road which leads south to Sonoyta, Mexico, thence on to Punta

Penasco, Sonora, Mexico. The Gulf of Lower California lies within 50 miles of the southern boundary of the Monument. Only one additional graded road is maintained and this runs along the southern border from the Monument Headquarters to Quitobaquito in the southwestern corner of the area, a distance of about 20 mi. Numerous unimproved desert roads lead to most sections of the Monument but are traversable only with proper equipment and then sometimes with difficulty.

The field study was initiated in July, 1948, and concluded the following season (February-August, 1949). The study was made possible through the courtesy of the National Park Service and with the generous cooperation of the local officials, William R. Supernaugh, Monument Superintendent and Ranger Glen L. Bean.

The writer is indebted to Dr. A. A. Allen, Department of Conservation, Cornell University and to Dr. S. Charles Kendeigh, Department of Zoology, University of Illinois, for their supervision of the research program and critical examination of the manuscript. Any errors are entirely the responsibility of the author.

Topography and Geology

Organ Pipe Cactus National Monument is a flat, level plain, interrupted by several ranges or groups of low mountains (Fig. 1). Most of the ranges extend in a north-south direction, which is the general pattern for northern Sonora, southeastern California, southern Arizona, and southern New Mexico (Gould 1938).

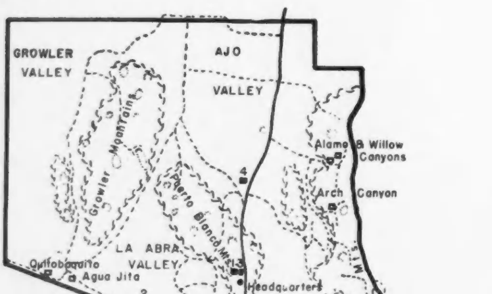

FIG. 1. Organ Pipe Cactus National Monument.

Two prominent mountain ranges are present within the boundaries of the Monument, the Ajo and the Growler Mountains. Several smaller groups are also included as well as four main valleys, the Ajo, Sonoita, La Abra, and Growler. For the most part the mountains are relatively low, and the entire Monument lies almost completely within the Lower Sonoran Life Zone. Only in the canyons of the Ajo Mountains does one approach Upper Sonoran conditions (Phillips & Pulich 1948). Santa Rosa, the highest peak of the range, rises to 4829 ft. Kino Peak, in the Growler range, has an elevation of 3057 ft. while Twin Peaks, highest of the Puerto Blancos, is 2600 ft.

The southern boundary of the Monument coincides with the northern boundary of the State of Sonora, Mexico, for its full length of approximately 32 mi. The eastern boundary extends for about 25 mi. along the crest of the Ajo Mountains where it contacts the Papago Indian Reservation. The western edge is a common boundary with the Agua Prieta Wildlife Refuge. The southern and northern boundaries have been almost completely fenced and the western border partly so. Fencing will eventually completely surround the Monument, with the exception of the Ajo Mountain sector, in order to prevent the ingress of cattle from adjoining range lands bordering on the north and south sides.

Most of the rocks within the Monument are of three general kinds; old pre-Cambrian schist, gneiss, and granite; Tertiary volcanic lava and tuff, and recent alluvium and valley wash (Gould 1938). The pre-Cambrian element is chiefly gray and red granite and schist. The greater part of the rocks which form the mountains are of volcanic origin for the region contained many volcanoes during the late northern Sonoran geologic period (Gould 1938). As the molten lava cooled it formed black basalt which is now exposed on the mountain tops. Lighter colored volcanic ash was compacted and hardened to form tuff. Layer after layer of these accumulated until thicknesses of 2000 ft. or more are attained as in the Ajo Mountains.

Large deposits of alluvium occupy the valleys. Rock debris and other materials washed from the mountains have filled the lower reaches to depths of hundreds of feet in some cases. This alluvium is sometimes cemented by lime or other materials to form a conglomerate, but most often in this region it is loose and unconsolidated. Caliche (hardpan) is formed in this region as a mixture of uncemented material (Breaziale & Smith 1950).

Natural Water Supply

Gould (1938) reported three springs on the Monument, namely: Bull Pasture Spring (Ajo Mountains), Dropping Springs (Puerto Blanco Mountains), and Quitobaquito. At least three additional sources of semi-permanent tinajas (pot-holes) have been recently located and two other permanent springs. The latter may have been included by Gould as part of the Quitobaquito Spring as Agua Jita is a seep of about 30 yd. approximately a half mile east of Quitobaquito and Rincon Spring is approximately three mi. north. The flow at Quitobaquito, estimated at about 43 gallons per minute by Gould, was impounded several years back by a Papago Indian who settled nearby and planted a few fruit trees in the vicinity. The pond now covers

about one-quarter of an acre in area and comprises a veritable oasis in the desert. The spot was formerly one of the major water holes along the old "Camino del Diablo" which ran from Sonoyta to Yuma during the early mining era of the southwest country.

During the current study several exploratory excursions were taken into the canyons of the Ajo Mountains where several semi-permanent shaded tinajas were discovered. Upper Alamo, "Willow," Arch, "Mammosa," and Canyon Diablo all contained pools of water that were with the exceptions of Diablo and Alamo accessible to the mammals and birds of the region. The names "Willow" and "Mammosa" are terms utilized by the writer as a temporary means of distinguishing the canyons for no names have been permanently applied.

In addition to these natural water sources, a total of at least six active wells are present. These are all fenced and are available only to the cattle and the smaller vertebrates.

CLIMATE

Latitude, altitude, interfering mountain ranges, and remoteness from any large body of water are the principal factors which influence the climate of the region. Temperatures are high and the rainfall low which accounts for an extremely low relative humidity. Temperature ranges between diurnal and nocturnal periods are great and generally speaking, the summers are usually long.

Temperature. Two weather stations, located near the Monument, present a reasonably accurate appraisal of conditions at the study areas. Ajo is ap-

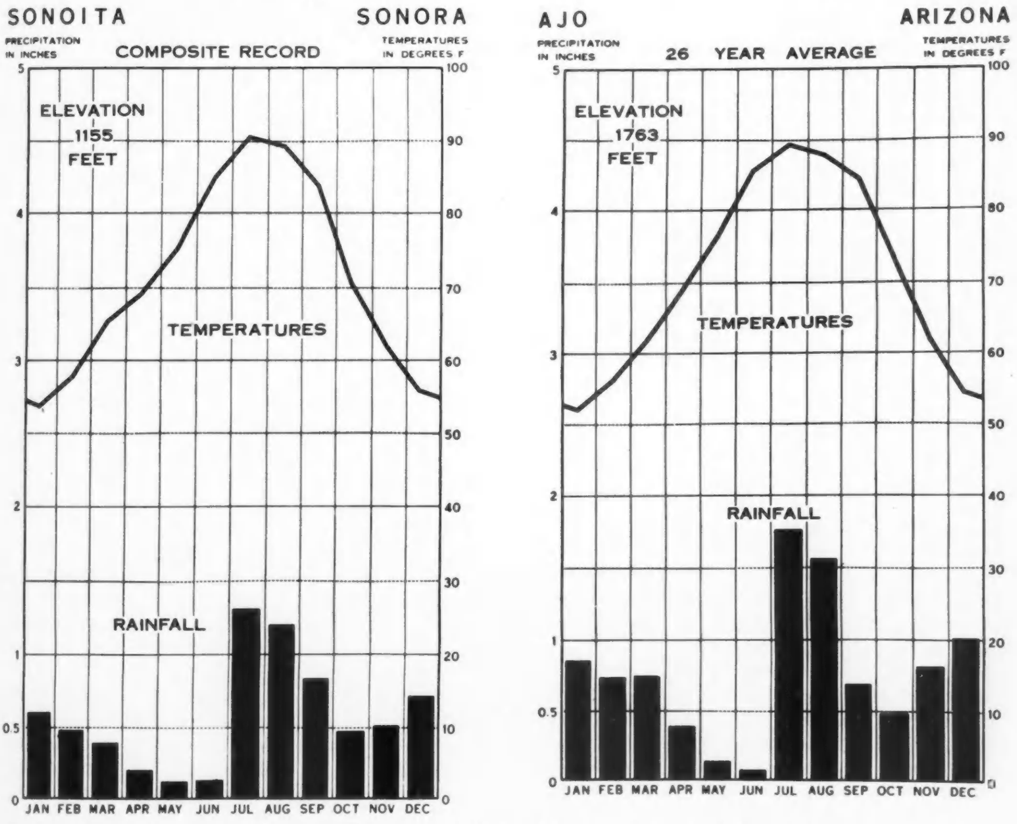

FIG. 2. Composite record of temperatures and rainfall at Sonoita, Mexico and Ajo, Arizona.

TABLE 1. Mean monthly maximum and minimum temperatures during the study period in 1948-49.

	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	April	May	June	July
Mean Maximum......	102.6	99.5	86.4	72.6	64.5	55	62	75.5	85.9	89.1	95.5	101.2
Mean Minimum.......	72.5	66.8	57.7	38.3	37.8	31.5	33.5	41	50.2	52.9	62.4	73
Mean Monthly........	87.6	83.2	72	55.5	51.2	43.3	47.7	58.3	68.2	71	78.9	87.1

proximately 30 mi. northwest of Monument headquarters while Sonoyta, Sonora, Mexico, is only about 5 mi. to the south. Figure 2 shows composite records for several years at these stations.

Daily temperature readings were also taken at Monument Headquarters. These data are shown in Table 1 for the months during which the current study was conducted.

The average date of the last spring frost at Ajo falls on January 22 and the average date of the first autumn frost comes on December 20. There is thus an average growing season of 332 days. Extreme frost dates are March 13 and November 11.

Precipitation. Two distinct rainy seasons are characteristic for the state as a whole with the most important season occurring during July, August, and September. According to Smith (1945) the state receives about 43% of the entire year's supply during this period. During the current study at Organ Pipe Cactus National Monument the summer rainfall came chiefly during the month of October, somewhat later than the mean season. These summer rains are spotty in distribution and spontaneous in nature, usually short-lived and accompanied by wind, thunder, and lightning. A total high for the month of October at Monument Headquarters amounted to 2.6 in.

The second rainfall period takes place from December to March and is of considerably longer duration but produces less water (35%) of the annual precipitation of the state. These rains are mostly gentle showers which may last for hours. Normal monthly and annual precipitation for Ajo and Organ Pipe Cactus National Monument is shown in Table 2.

Miscellaneous Climatic Phenomena. The Sonoran region lies in a belt of lower relative humidity than most other parts of the United States. On hot summer days the relative humidity may go as low as 5% or less. As to be expected the winter months may have quite high humidity records due to the lower temperatures and the occurrence of the winter rainy season. Highest humidity may be expected just before sunrise during the normal daily fluctuating cycle and a low point is usually reached just after noon, depending on the temperature.

The southwestern sector of Arizona receives more sunshine than does any other part of the country. Here approximately 85% of the possible sunshine is recorded. The winter months of November, December, and January produce the lowest number of sunny days as a rule.

Wind velocities are mild, usually ranging from 5 to 8 mi. per hour, depending on the local topography, while extreme velocities seldom reach fifty miles per hour. The prevailing winds are from the southwest. Ajo records prevailing winds from the south for January and November.

VEGETATIONAL ASPECT OF ORGAN PIPE CACTUS NATIONAL MONUMENT

Benson & Darrow (1944) place the southwestern creosote bush deserts into three categories (Mojave, Sonoran, and Chiuahuan) arranged according to species composition and general structure of the vegetation. According to these workers the Arizona Desert differs from the other southwestern deserts in the richness of its arboreal and succulent plants, being partially isolated from the other deserts by the low elevations of the Colorado River on the western border and by the higher elevations of the Mexican Plateau between southeastern Arizona and southwestern New Mexico.

The term biome is used as a synonym of biotic formation which essentially is a complex of fully developed and developing communities, characterized by uniformity of the plant climaxes. The biome (Clements 1946), is based upon both plants and animals.

Although covered primarily by such characteristic desert plants as creosote bush, bur sages, etc., many minor variations in the vegetation exist within the Monument due to differences in soil composition, texture, available moisture, shade, and altitude. The lowest elevation (1000 ft.) on the Monument is found in the extreme southwestern sector around Quitobaquito and Agua Jita. Only here are found such plants as arrow weed (*Pluchea sericea*) and smoketree (*Dalea spinosa*). On the other hand, the shaded canyon floors of the Ajo Mountains may exceed 4000 ft. in elevation and support a host of plant species entirely restricted to such specific situations. Juniper and oak trees are common in the canyons and such herbs as the gooseberry (*Ribes quercetorum*) and *Penstemon microphyllus* may be found in association with the Vauquelina.

A total of 398 species of plants have been recorded by the local officials to date (1950) on the Monument and represent 72 families.

Many of the plants are of unusual interest for they represent new locality records and include range extensions of considerable distances. Few professional botanists have visited the region and, as a result, the flora of the Ajo Mountain canyons, in particular, is not well known. Many plants of more than causal interest are certain to be found once the hardships of

TABLE 2. Normal monthly and annual precipitation for Ajo and Organ Pipe Cactus National Monument.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
Ajo (27 yrs.)	.84	.71	.66	.30	.11	.11	1.48	1.85	.97	.50	.70	1.06	9.29
Organ Pipe (5 yrs.)	.45	.56	.55	.12	.01	0	.66	1.81	2.11	.70	.65	.89	7.69
Organ Pipe (1948-49)	2.19	.06	.37	.22	0	T	.65	.90	.07	2.64	0	1.14	8.24

desert remoteness and discomforts are braved by some interested scientists. *Agave schottii* var. *treleasei*, known only from one station on the southern slopes of the Santa Catalina Mountains and the bush penstemon, *Penstemon antirrhinoides* var. *microphyllus* (nearest locality 150 mi. to the northeast) are two of the unusual plants found in the canyons of the Ajos. The elephant plant, *Bursera microphylla*, occurs along the foothill slopes near Sweetwater Pass in the south central part of the Monument. Colonies of *Dalea pringlei* and *Jatropha angustidens* were found in Arch Canyon in 1947 by C. L. Fouts but have since disappeared so their inclusion in the flora of the Monument is questionable at this time.

The small pond at Quitobaquito supports a fine stand of sedge, *Cyperus laevigatus*, which was first collected by Mearns during the early expeditions of the International Boundary Survey. Four miles to the north at Rincon Springs is another small water hole (mentioned earlier) that has a flourishing stand of cattails.

Two major eco-systems or soil-vegetation complexes are found in the Monument, namely: (1) alluvial fill and (2) the lava-granite composition of the mountains.

INTERMOUNTAIN ALLUVIAL FILL COMPLEX

Most of the valleys or intermountain plains are composed chiefly of silt and rocks washed down from the adjoining mountain ranges. Varying degrees of consistency and composition of the alluvial

FIG 3a. View looking west from the mouth of Alamo Canyon.

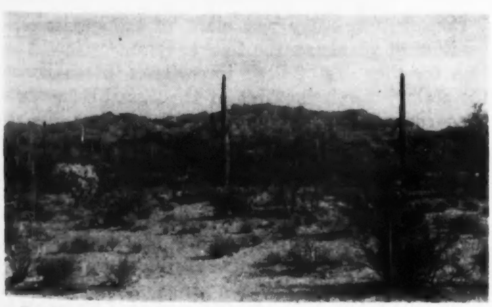

FIG 3b. View looking northeast from Monument Headquarters.

Photos by courtesy of Wm. R. Supernaugh

fill are present and may influence the vegetation type growing on them depending on the exposure, available moisture, altitude, and other factors (Fig. 3).

On the western edge of the Monument, west of the Growler Mountains and in the eastern extremity of the Colorado Desert, the soil apparently has a larger gravel content, and is generally more arid. Plants are widely spaced, the vegetation is less luxuriant, and competition for water is obviously keen. There are few saguaros (*Cereus giganteus*) and large trees. Three chollas are present: *Opuntia acanthocarpa*, *O. arbuscula*, and *O. ramasissima*. The barrel cactus, *Echinocactus wislinzenii* occurs only in this area. Creosote bush (*Larrea divericata*) is the dominant plant. Within this area, stands of Hilaria are present.

Where the silt is fine and sandy, such as the Ajo Valley and along the northern portion of the Monument, several species have reduced numbers. Saguaro, iron-wood, and palo verde trees occur only in scatterred regions. Creosote bush occurs in large pure stands that reach their maximum development on the Monument. Also an extensive mesquite bosque (forest) is found in the northern sector of this silty soil-type. The crucifixion thorn (*Holacantha emoryi*) and the showy Ajo lily (*Hesperocallis undulata*) are common.

South of the Puerto Blancos on the eastern edge of La Abra Valley lies quite a different faciation. Here are concentrated the large stands of mature saguaros. The alluvium is liberally sprinkled with granite particles from the adjoining mountains and this provides a heavier, more stable soil for the roots of the giant cacti. Along the southern slopes of washes and foothills are also found the prominent and conspicuous organ pipe cactus, (*Cereus thurberi*), and in the lower wash floodplains an occasional specimen of the rare senita (*Cereus schottii*) may be encountered. In the northeastern portion of the Monument of the same general soil type but at a somewhat higher elevation such plants as yucca (*Agave schotti*), desert willow (*Chilopsis linearis*), desert honeysuckle (*Anisacanthus thurberi*), and *Opuntia kunzii* are found.

Most of the remaining alluvial fill soils may be classed as caliche or conglomerate and comprise the larger part of the intermountain plains, including the Sonoyta Valley. Covered by the everpresent Larrea and Franseria they also support a great variety of chollas, as well as ironweed, desert hackberry, palo verde, catclaw, and many other species.

Where permanent standing water is present, such as the situation at Quitobaquito and Agua Jita, a great variety of plants may be found immediately surrounding the periphery of the area. Black willow (*Salix nigra*) and several large mature specimens of the cottonwood (*Populus fremontii*) grow around the small pond at Quitobaquito. A few specimens of the screwbean mesquite, *Prosopis odorata*, may also be found here. The seepage at Agua Jita supports a fine stand of honey mesquite, *Prosopis juliflora*;

catclaw, *Acacia greggii* and the conspicuous annual jackass clover, *Wislizenia refracta.*

Mountain Lava-Granite Complex

The Ajo Mountain range provides one of the most distinctive vegetational units on the Monument. Numerous species are found only in the shaded canyons and along protected ledges of the higher elevations. Such tree species as juniper (*Juniperus monosperma*), desert olive (*Forestiera phillyreoides*), Arizona rosewood (*Vauquelinia californica*), and Palmer's oak (*Quercus palmeri*) grow in the canyons. A host of shrubs grow profusely on the canyon floor and around the occasional water-seepage areas. Saguaros, organ pipe cactus, prickly pears, creosote bush, palo verde, and many other species are found over most of the mountain slopes and often extend to the tops when enough soil is available to hold the roots.

DESCRIPTION OF THE STUDY AREAS

Topography and Location

Four typical lower Sonoran desert areas were studied intensively in so far as the plant composition and bird populations were concerned. During the course of the initial survey of the Monument, and in conducting the censuses throughout the summer, some 1800 miles were traveled by auto, truck, and on foot in the process of accumulating the data. Many of the isolated mountain ranges were reached only by extensive hikes and the necessity of packing water and food made frequent trips impractical. However, two canyons (Alamo and its adjoining branch "Willow") were readily accessible and frequent bird censuses were conducted in them during the breeding season. Three extended exploratory surveys to the more remote canyons in the Ajos were made with Monument officials and an opportunity was thus available for a general appraisal of the plant and avian constituents. These trips marked the first exploration of the canyons since the Monument was established in 1937.

The primary objective of the study was to determine the breeding-bird composition of the desert floor. An attempt was made to select accessible study areas containing as many of the habitat-niches as possible that were present in the extensive intermountain plains of the desert. Special consideration was therefore directed toward the dry washes or arroyos. their adjoining "outwashes," and intervening desert country. These intermountain alluvial plains are dissected by innumerable dry washes running from the mountains and their foothills to the larger washes at lower elevations. It is difficult to find any large area devoid of the typical thin belt of mesquite, ironwoods, and associated plants that accompany even the smaller washes. At least one study plot was located in each of three major valleys of the region namely: the Ajo, Sonoyta, and La Abra (Fig. 1).

Of the four areas finally selected two (1 and 2) represent examples of the larger dry washes and two (3 and 4) of areas with only small tributaries, being, primarily, sections of the flat desert floor.

Area 1. Located a quarter mile north of headquarters in the Sonoyta Valley, this 70 ac. rectangular tract embraced a typical dry wash and its adjoining low hinterland. A narrow fringe of mature mesquites and ironwoods paralleled the bed of the ten to fifteen foot-wide sandy wash. The adjoining region was sprinkled with saguaro, chain cholla, creosote bush, and bur sages, common constituents of the desert floor. The trees along the wash ranged in height from 15-35 ft.

Area 2. This 40 ac. plot is the second wash area and is located in the La Abra Valley south of the Puerto Blanco Mountains approximately 10 mi. from headquarters along the desert road to Quitobaquito. Its southern boundary parallels the Mexican border 300 yds. to the the south. Floristically it is similar to the first area discussed. It contains a sizable dry wash lined with mature trees. Being in the belt of the mature saguaro stands along the southern boundary it contains a substantially larger and more mature giant cactus component.

Area 3. In contrast to the above study plots this area is a 100 ac. expanse of the typical general desert floor. Located immediately to the west and bordering Area 1, it provides an excellent comparative relationship to the wash situation. The remaining three sides (north, west, and south) are bordered by hills of the Puerto Blanco Range thus creating a more or less natural boundary. The topography is that of a gentle slope from the hill on the west boundary eastward to the wash in Area 1. No one large wash occurs within the area, but it is traversed by a series of small drainage channels all running to the eastward.

Area 4. In the Ajo Valley some eight miles to the north of Monument Headquarters lies a 50 ac. tract of pure creosote bush. No drainage wash crossed the area. It is typical of the large flat reaches characteristic of the fine sandy silt of the Ajo Valley. A few straggly mesquites line the northern boundary and a small wash runs a few hundred feet south of the southern border line. Only one dead mesquite stump lies within the area.

Flora

Considerable study was made of the species composition of plants on the four areas under consideration for they are of basic importance in considering the ecological relationships of the faunal components of a community. An analysis of the flora was attempted by counting and recording each individual of the species encountered. In the case of the wash areas (1 and 2) the main bed was followed and every plant along both sides recorded. Percentages derived from such data are for practical purposes almost absolute. A somewhat different procedure was used in Area 3. Here a series of three transects were laid out across the area and on each of these was located three plots measuring 100 ft. on a side. These plots were selected at random in order to

TABLE 3. Plant species composition of four selected Lower Sonoran Desert areas.*

Species	Combined total No. Counted	%	Area 1 Number Counted	%	Area 2 Number Counted	%	Area 3 Number Counted	%
Franseria deltoidea (Bur-sage)	1096	19.0	175	10	72	5	849	30
Larrea divericata (Creosotebush)	763	13.0	281	16	132	10	350	13
Cercidium microphylium (Yellow Palo-verde)	594	10.1	31	2	70	5	493	18
Cereus giganteus (Saguaro)	497	9.0	208	12	255	20	34	1
Franseria ambrosioides (Bur-sage)	363	6.0	289	16	74	6	–	–
Lycium parishii (Desert Thorn)	350	6.0	146	8	168	13	36	1
Acacia greggii (Catclaw)	269	4.6	151	9	108	8	10	.5
Olneya tesota (Ironwood)	251	4.2	23	1	84	7	144	5
Opuntia fulgida (Chain Cholla)	195	3.3	174	10	+	+	21	1
Acacia constricta (White-thorn)	182	3.0	43	2	–	–	139	5
Celtis pallida (Desert Hackberry)	137	2.3	94	5	11	1	32	1
Hymenoclea pentalepis (Burro-bush)	131	2.2	–	–	131	10	–	–
Sapium biloculare (Jumping Bean)	130	2.2	–	–	–	–	130	5
Encelia farninos (Encelia)	127	2.1	–	–	15	2	112	4
Opuntia bigelovii (Teddy Bear Cactus)	119	2.0	–	–	–	–	119	4
Cercidium torreyanum (Blue Palo-verde)	91	1.5	46	2	43	4	2	+
Condalia globosa (Bitter Condalia)	86	1.5	50	3	34	3	2	+
Prosopia juliflora (Mesquite)	68	1.1	17	1	48	4	3	+
Opuntia acanthocarpa (Staghorn Cholla)	66	1.1	–	–	–	–	66	3
Jatropha cardiophylla	66	1.1	–	–	–	–	66	3
Lycium berlandiere (Lycium)	52	1.0	–	–	–	–	52	2
Fouquieria splendens (Ocotillo)	49	.8	–	–	–	–	49	2
Bebbia juncea	38	.6	36	2	2	–	–	–
Krameri grayi	333	.5	–	–	–	–	33	1
Calliandra eriophylla	31	.5	–	–	–	–	31	.5
Anisacanthus thurberi (Desert Honeysuckle)	23	.4	23	1	–	–	–	–
Condalia lycioides (Sweet Condalia)	21	.4	–	–	19	1	2	–
Jatropha spathulata	14	.2	–	–	–	–	14	1
Jatropha canescens (Dragon-blood)	9	.1	–	–	9	1	–	–
Opuntia arbyscula (Pencil Cholla)	6	.1	–	–	–	–	6	.5
Krameria parvifolia	5	+	–	–	–	–	5	+
Atriplex canescens (Fourwing Saltbush)	4	+	–	–	4	+	–	–
Funastrum heterophyllum (Trailing Milkweed)	4	+	2	+	2	+	–	–
Cereus thurberi (Organ Pipe Cactus)	4	+	–	–	–	–	4	+
Echinocereus Engelmanii (Hedge-hog Cactus)	3	+	–	–	–	–	3	+
Echinocactus Wislizenii (Barrel Cactus)	2	+	–	–	–	–	2	+
Total No. of plants recorded	5879		1789		1281		2809	
Total No. of species recorded	36		17		20		29	

*Area 4 composed of 100% creosotebush (*Larrea divericata*).

represent as unbiased an appraisal as possible. All plants were counted within each of the 0.23-ac. plots and from the composite total of the nine plots the percentage of occurrence of each species was recorded. In addition short randomly selected sections of three of the larger drainages were checked in order to get a representative portion of the wash species. Two plot counts were also made in Area 1.

Thirty-six species of plants comprise the major part of the vegetation on the areas under consideration (Table 3). Bur sage, creosote bush, yellow palo verde, and the saguaro are the most abundant species ranking in the order listed. It is apparent that this region falls into the Larrea sub-type of the Larrea-Atriplex association as defined by Nichol (1943). The conspicuous occurrence of the saguaro and chain cholla (*Opuntia fulgida*) further defines the area as part of the Arizona Succulent Desert as described by Kearney & Peebles (1951).

Examination of Table 3 provides one a clear idea of the vegetation of each research area. The common creosote bush and bur sage (*Franseria deltoida*) make up the "matrix" of the vegetation pattern, being well represented in all three localities. Of the tree species, catclaw, and bitter condalia (*Condalia globosa*) are about equally represented in the two wash areas. The abundance of other trees varies considerably.

The two species of palo verde present an interesting correlation. The blue palo verde (*Cercidium torreyanum*) is quite sensitive to the moisture factor. Area 2 being almost completely an out-wash situation has twice the percentage of this species as does Area 1, which is somewhat higher and drier. This species is almost exclusively a wash inhabitant. The yellow palo verde (*C. microphyllum*), on the contrary, is found on the uplands where its greatest numbers are recorded in abundance in the upland research area (3). Other predominately wash plants are *Franseria ambrosioides* and *Lycium parishii.*

Most conspicuous is the difference in abundance of the saguaro. Scattered sparingly, but still being

a prominent feature of the landscape in Area 3, they reach a peak in the low wash situations (Area 2) comprising 20% of the total species composition and being the most abundant species. Making up 12% of the total in Area 1, the saguaro ranked third in abundance.

The chain cholla was, by far, more abundant in Area 1 than in either Areas 2 or 3 (Table 3).

BREEDING BIRD POPULATIONS OF THE RESEARCH AREAS

METHODS OF STUDY

The major part of the field research was devoted to determining the breeding bird populations of the desert floor or intermountain plains. Owing to their significance, limited time was also spent in censuing areas around sources of natural permanent water and, to some extent, in the more accessible mountain canyons of the Ajos. Ninety six censuses were conducted on the four research areas, at Quitobaquito, and in Alamo and "Willow" Canyons (Table 4). In addition a single census was taken in three remote canyons (Arch, April; Diablo, May 6; and "Mammosa," June 12) and four others at Aqua Jita (April 7 through July 24). A total of 102 censuses was made involving 348 man-hours. During the time spent on the areas 132 nests were located, which when added to the 52 additional ones found while traveling about the Monument and to the study areas, makes a total of 184 active nests. Of this number approximately 125 were examined periodically and detailed information recorded.

Following the census trips about 300 man-hours were spent in searching for nests and data gathered concerning the nest building, attentiveness of the nesting individuals, incubation, care of the young, and territorial behavior of the various species.

Censusing of the four intermountain areas was accomplished by the combination of the strip, plot, and nest counting techniques described by Kendeigh (1944). Census lines were marked out across the study areas and by alternately following the lines and the areas between a thorough coverage was guaranteed. Chances of recounting individuals over sections already covered were thereby minimized. The census lines, ranging from 120 to 250 ft. apart, depending on the terrain and vegetation, were marked by colored cards (3 x 6) which were tied to conspicuous plants. Each card bore a letter which denoted the census line and a number indicating the position on the line. Scaled field maps of the areas were then mimeographed with the check points included, thereby making it possible to locate exactly any individual recorded during the census trips. Particular effort was made to plot all singing males and nests located.

Composite maps were made for each species from these data and by merely encircling the clustered recorded locations of the individuals it was relatively simple to determine the number of territories present for each one. By combining the various species one could then determine the total breeding density for the area concerned. The sizes of the various territories were determined by the use of a planimeter. For those species not exhibiting territorial behavior the presence of nests, young, and other criteria were necessarily considered in evaluating their population density.

The canyon censuses were made primarily to record the species and all nests possible. An attempt was made to determine the relative breeding density for comparison with other canyon studies. Approximate densities were derived from the accumulated data. Usually only one passable trail was present in the canyons. Consequently, all recordings of species and numbers were made while progressing up the canyon while the downward trek was devoted primarily to searching for nests and observations.

At Quitobaquito and Agua Jita one merely had to traverse the circumference of the pools and record the birds as they came in to drink or bathe. No particular concentration of nests or territories was evident around these areas.

The breeding populations of the various study plots are treated in the following categories.

NESTING SPECIES AROUND PERMANENT NATURAL WATER SOURCES

As would be expected a source of available water in such an arid region attracts great numbers of individuals. Due probably to such constant influxes of birds seeking relief from the heat and thirst few

TABLE 4. Compilation of census data on the research areas.

Research Area	Total Number Census Trips	Total Number Census hours	Total Number Breeding Species	Total Number Trans. or Visit.*	Total Number Nests Found	Extreme Census Dates
Area 1	25	100	16	27	48	Mar. 6 - July 27
Area 2	15	45	17	17	33	Mar. 16 - July 19
Area 3	21	126	15	4	22	Mar. 7 - July 27
Area 4	10	20	0	14	0	April 1 - July 2
Alamo Canyon	6	18	20	19	15	Mar. 17 - July 28
Willow Canyon	4	12	16	14	4	May 15 - June 30
Quitobaquito	15	15	15	45	10	Feb. 28 - Aug. 24
Totals	96	336	..	..	132	....

(*) Transients or visitants.

TABLE 5. Species and numbers of birds recorded at Quitobaquito from February through June (1949) and August (1948).

	Feb.	Mar.		April			May					June		Aug.
Species	28	26-	29	7-	17-	29	4-	9-	13-	25-	27	7-	16	24
Pied-billed Grebe				1	1									
Treganza's Heron												1		
Anthony's Green Heron	1	1	1	1				1	1					
Wood Ibis													1	1
Mallard					1									
Green-winged Teal	2			1										
Blue-winged Teal				2					2					
Cinnamon Teal								1	1					
Red-head				1										
Greater Scaup		1												
Turkey Vulture			1						1					1
Black Vulture		1												
Cooper's Hawk				1										
Red-tailed Hawk								1						
Gambel's Quail				1		4		1			2	10		
Sora						1		1						
Coot						1								
Killdeer	15	6	6	8	6	6	8	1	4	1	2	2		5
Wilson's Snipe	4		2	2										
Spotted Sandpiper								1						
Solitary Sandpiper				1		1		1						
Western Sandpiper				2	8									
Western Mourning Dove		8	6	7	6	4	10	12	3	15	10	4	2	
White-winged Dove						1	6	10	2	100	400	400	200	
Texas Nighthawk										1		2	1	
Belted Kingfisher					1									1
Gila Woodpecker	1	1	1					1	1					
Western Kingbird								4	2					
Ash-throated Flycatcher						2	2	1		2				
Western Flycatcher								1						
Black Phoebe	2	1				1					1			2
Vermilion Flycatcher		1	2	1			1	1	1	2			2	
Violet-green Swallow		2								1	1			
Tree Swallow		4												
Cliff Swallow										2			8	
Rough-winged Swallow														28
Barn Swallow										2				
Verdin										1	1	1		
Mockingbird	1	2	1	2	2			4	1	2				
Palmer's Thrasher	1		2							1	2	1		
Crissal's Thrasher										2	1			
Robin	1	1												
Phainopepla	2		4	5	4		3	6	2	4	4	1		
Least Vireo						2	1	1	1	3	1	1	1	
Solitary Vireo	1													
Yellow Warbler				1	2	2				1				
Audubon's Warbler		1												
Yellowthroat		1												
Pileolated Warbler		2	4	1	4	8	4	2		2				8
Western Meadowlark				4										
Yellow-headed Blackbird								1						
Hooded Oriole		2	1	4	2	4	3	2	2	2	4		1	2
Dwarf Cowbird		2				25		25	25	50	40	25	50	
Black-headed Grosbeak													1	
House Finch								5		25		6		
White-crowned Sparrow	10	12	15						2					
Gambel's Sparrow									2					
Total Numbers	63	66	65	96	37	62	38	83	52	221	477	444	265	54
Total Species	14	18	13	20	11	14	9	22	16	21	13	11	8	9

birds nest in the immediate vicinity of the pond at Quitobaquito. Only about 15 species of the 59 recorded were found to be nesting nearby (Table 5) and only one pair of each species usually was the case, with the exception of the two dove species (white-winged and mourning doves), hooded oriole, and killdeer. The spring supplying the flow of water emerges to the surface about 100 yds. away from the pond and flows down a slight incline to the impoundment. The tiny stream is only about a foot wide for most of its length but around the spring and along the flow a rather luxuriant growth of condalia and mesquite flourish, as well as, stands of arrow weed, lycium, and other smaller plants. These furnished a suitable cover for white-winged and western mourning doves to congregate by the hundreds in some cases. Many of these birds nested in the surrounding hinterland and came in regularly for water but most of the individuals were migrants. Concentrations of white-winged doves on four censuses during latter May and early July (Table 5) numbered 100, 400, 400, and 200, respectively. Mesquite and condalia trees on such occasions would be crowded with resting birds while new arrivals constantly dropped in while others were leaving for their nesting or feeding sites. Western mourning doves were not so numerous as its relative, discussed above, but on occasions as many as 15 would be seen during one observation at this spot.

Two pairs of hooded orioles nested in the cottonwoods bordering the pond. One pair had a nest about 7 ft. from the ground on the north side while the nest of the second pair was placed 12 ft. up in a cottonwood on the west side of the pond. Chasing by the males was observed only on two occasions. Both pairs nested successfully.

Huey (1942) stated "About a dozen Killdeer lived about Quitobaquito where conditions were ideal for them." During the current study, only six individuals were regularly recorded and only one pair was observed with young.

A single pair of vermilion flycatchers evidently controlled all nesting rights for this species around the pond. The adults were often seen flying low over the water or darting out for insects from favorite perching sites atop a dead mesquite tree. Both adults were seen feeding three fledglings on May 25.

One verdin nest was found along the little steam and apparently was the only nesting pair in the vicinity.

Gambel's quail came to water regularly and on one occasion (May 27) five pairs were recorded. One female was observed on May 4 in the process of shaping a nesting cavity under a small bush along the small stream but deserted the site after being flushed. A pair with 12 young chicks was feeding near the pond on May 9, evidently having nested in the near vicinity.

Young mockingbirds and Crissal's thrashers were recorded on May 25. This pair of Crissal's thrashers and the three fledglings marks the only nesting observation of this species during the study. Huey found a nest containing one fresh egg on March 25 at this location and collected a fully feathered bird of the year at Bates well on April 25.

Four censuses were taken at nearby Agua Jita. The short seepage here did not afford such an im-

portant source of food as did the pond at Quitobaquito but was utilized extensively for drinking and bathing purposes. The accompanying stand of mesquite, catclaw, and condalia was much denser and afforded well protected nesting sites. The same situation existed here as was found at the other water locality. Concentrations of birds were high while nests were again not in evidence. Only three nests (western mourning dove, Gambel's quail, and Arizona crested flycatcher) were observed. The single nest of the Gambel's quail, which contained 21 eggs, was the only one located for the species during the study. At least eight pairs of these birds apparently nested in the vicinity for four pairs were seen at the seepage on April 29, including a brood of several young chicks, while as many more were calling nearby.

A single nest of the western mourning dove was located deep within the thicket, 8 ft. high in a mesquite while the pair of crested flycatchers occupied a woodpecker hole in a saguaro nearby.

A total of 21 species was recorded at Aqua Jita from April 7 through July 24. Of this number, five species were found here but not seen at nearby Quitobaquito (Arizona crested flycatcher, cactus wren, Sonora gnatcatcher, Arizona Bell's vireo, western warbling vireo, bronzed cowbird).

The greatest concentrations were noted on the June 16 (12 species, 192 individuals) and July 24 (10 species, 189 individuals) visits.

SPECIES COMPOSITION AND RELATIVE POPULATION DENSITY OF THE MOUNTAIN CANYONS

Six censuses were conducted in Alamo Canyon (Table 6) during which time a total of 38 species of birds were recorded. Of this number at least 20 are known to constitute the breeding component. An area about 25 by 800 yds. in width constituted the accessible census area of the canyon. During the previous summer (July, 1948) an exploratory hike was made into upper Alamo Canyon and here was recorded the first positive nesting record for the pyrrhuloxia on the Monument. Two adults and three feathered fledglings were observed in dense brush that lined the banks of the wash along the canyon floor. This species was not recorded during the following season (1949) but their niche was apparently occupied by a pair of cardinals which were recorded on each census in the same locality. Rock and canyon wrens were present and a pair of each species was observed carrying nesting material into crevices of the steep rocky walls.

On July 28 an adult ferruginous pygmy owl with two fully grown young was observed midway up the canyon. This record with the pair that nested on Area 1 also constitutes a new nesting species for the Monument. Two pairs of hooded orioles occupied territories in Alamo and both reared young.

TABLE 6. Species composition and relative population density of Alamo Canyon.

Species	March 17	March 24	April 10	May 21	June 30	July 28
Turkey Vulture	..	..	..	1	..	..
Harris's Hawk	1	..	..	..	..	..
Sparrow Hawk	..	..	..	1	..	..
Gambel's Quail	8	5	4	8	8	30
W. Mourning Dove	1	4	20	100	50	20
White-winged Dove	..	..	..	44	13	10
Roadrunner	..	..	..	1	..	..
Ferruginous Pygmy Owl	..	..	..	..	..	1
Costa's Hummingbird	1	2	..	5	..	..
Gilded Flicker	2	2	..	..	..	..
Gila Woodpecker	..	..	..	..	..	1
Ladder-backed Woodpecker	1	1	..	..	2	1
Arizona Crested Flycatcher	1	2	..	4	10	..
Western Flycatcher	1	2	..	1	..	..
Black Phoebe	1	..	..	..	..	..
Raven	2	..	..	..	..	2
Verdin	3	3	1	14	3	3
Cactus Wren	1	2	..	..	..	..
Canyon Wren	3	1	..	..	3	2
Rock Wren	1	8	2	..	..	2
Palmer's Thrasher	1	4	3	9	..	3
Sonora Gnatcatcher	2	4	..	6	2	..
Ruby-crowned Kinglet	6	6	..	..	..	..
Cedar Waxwing	..	..	..	1	..	..
Phainopepla	1	5	4	6	..	..
Orange-crowned Warbler	4	..	..	..	..	..
Calaveras Warbler	..	3	..	..	..	..
Black-throated Gray Warbler	..	4	..	..	..	..
Hooded Oriole	..	3	..	..	..	..
Scott's Oriole	..	..	..	..	..	1
Cardinal	1	4	2	2	1	2
House Finch	13	3	20	50	10	4
Green-backed Goldfinch	..	2	..	2	..	..
Brown Towhee	..	1	..	..	..	..
Desert Sparrow	..	4	4	..	..	..
Sage Sparrow	..	1	..	..	..	..
Pink-sided Junco	1	..	..	..	..	..
Brewer's Sparrow	..	..	2	..	..	..
Total Number Individuals	56	76	62	255	107	85
Total Number Species	22	24	10	17	11	15

Large contingents of western mourning and white-winged doves were also recorded here during the May and June trips. The majority of individuals were probably transients but many were inhabiting the surrounding hinterland. No nest of the former species was located and only three of the latter were found in the canyon. The cattle trough at the mouth of the canyon was undoubtedy the factor responsible for the large numbers of these species.

The Palmer's thrasher nests in the canyon were in chollas and regularly located along the length of the canyon.

Four pairs of Gambel's quail apparently comprised the breeding population of that species.

The breeding component of "Willow" Canyon was made of largely the same species as were found in Alamo. It was in this area that the first Grinnell's water thrush was recorded on the Monument. Of particular significance is the large numbers of doves of both the species discussed earlier. Highest densities were, as before, recorded during the May and June trips.

SPECIES COMPOSITION AND BREEDING DENSITY OF THE INTER-MOUNTAIN PLAINS

WASH AREAS (1 AND 2)

Thin lines of trees edging the widespread network of washes over the desert floor provide habitats for a great number of bird species. Utilized by the larger percentage of breeding individuals, these dry washes are also well marked migratory avenues for the transient species (Table 7). A total of 295 transient individuals through the two wash areas were recorded during the 78 day migration period. These individuals represented some 18 different species.

Two species (ferruginous pygmy owl and desert sparrow hawk) appeared as breeding species in Area 1 but not in the second area, although the sparrow hawk was a frequent visitant. Conversely four species (ash-throated flycatcher, western mourning dove, Sonora white-rumped shrike, and Mexican ground dove) were nesting in Area 2 but were not found to be inhabiting Area 1. Two additional species (western red-tailed hawk and western horned owl) had nests along the opposite boundaries of Area 2, on the east and west sides, respectively.

The difference in the population density of the two areas is largely due to the preponderance of white-winged and mourning doves nesting in Area 2 (Table 8). The density per 100 ac. of the first mentioned species in the second area was over twice that of Area 1. Furthermore no western mourning doves nested in the first area as contrasted to the 13 pairs per 100 ac. in the second study plot.

INTER-WASH AREAS (3 AND 4)

Considering first the migrant species as found on these types it is apparent that the absence of the wash vegetation is expressed by the numbers of species utilizing the open desert. A total of six species migrated through Area 3 while only three traversed the creosote bush area (Table 9). A total number of 165 transients recorded is also considerably smaller than the 295 found in the wash areas although the total area considered is at least 40 acres larger. Brewer's sparrows are by far the most abundant species for the dry creosote flats afforded by these areas are preferred by these birds. The nine records of violet-green swallows are individuals flying overhead in Area 3.

As is to be expected the breeding density of the open desert regions are not as high as the wash situations. Only 37 pairs per 100 ac. were present in Area 3 (Table 8) while the creosote flat was entirely devoid of nesting species. The occurrence of the three species (rock wren, canyon wren, and canyon towhee), are due to the presence of the surrounding hills of the Puerto Blanco Mountains as explained earlier. Actually, therefore, 23 species util-

TABLE 7. Migrant species showing periods recorded on the Wash Areas (1 and 2).

Species	Date first recorded	Date last recorded	Total period recorded	Total number recorded
Sage Thrasher	March 3	March 3	1 day	1
Cassin's Vireo	" 6	" 6	1 day	1
White-crowned Sparrow	" 6	April 13	38 "	160
Brewer's Sparrow	" 8	" 30	53 "	88
Pileolated Warbler	" 10	" 30	51 "	11
Western Flycatcher	" 27	July 27	122 "	7
Western House Wren	April 1	April 1	1 "	1
Gambel's Sparrow	" 1	" 1	1 "	1
Black-throated Gray Warbler	" 5	" 16	11 "	5
Yellow Warbler	" 5	" 24	19 "	5
Least Flycatcher	" 6	" 19	13 "	2
Scott Oriole	" 8	July 28	111 "	4
Clay-colored Sparrow	May 4	May 4	1 "	1
Lark Bunting	" 4	" 4	1 "	1
Western Tanager	" 4	" 12	8 "	2
Bullock's Oriole	" 5	" 12	7 "	3
Willow Thrush	" 20	" 20	1 "	1
Macgillivary's Warbler	" 20	" 20	1 "	1

Total migration period recorded March 3 - May 20 - 78 days*
Total number migrating species recorded - 18
Total number of migrating individuals - 295

(*) Last recorded dates of Western Flycatcher and Scott's Oriole not included.

TABLE 8. Breeding bird populations in four areas of typical Lower Sonoran Desert.*

Species	Area 1 (Wash) 70 acres	Area 2 (Wash) 40 acres	Area 3 (Open Desert) 100 acres	Area 4 (Creosote) 50 acres
Turkey Vulture	V	V	V	V
W. Red-tailed Hawk	V	.5 (1)	V	V
Harris's Hawk	V	V	V	–
Desert Sparrow Hawk	1 (1)	V	V	–
Gambel Quail	8.5 (12)	3 (8)	– (–)	V
W. Mourning Dove	V	5 (13)	V	V
White-winged Dove	9 (13)	11 (28)	7 (7)	–
Mexican Ground Dove	–	1 (3)	–	–
Saguaro Screech Owl	–	–	V	–
Western Horned Owl	–	.5 (1)	–	–
Ferruginous Pygmy Owl	1 (1)	–	V	–
Elf Owl	V	–	–	–
Costa's Hummingbird	V	V	V	–
Mearn's Gilded Flicker	+ (–)	– (–)	– (–)	–
Gila Woodpecker	2.5 (3)	2 (5)	2 (2)	–
Cactus Woodpecker	V	V	V	–
Ariz. Crested Flycatcher	2.5 (3)	2 (5)	2.5 (3)	V
Ash-throated Flycatcher	+ (–)	.5 (1)	1 (1)	–
Say's Phoebe	–	–	V	–
Purple Martin	–	V	–	–
Raven	–	V	–	–
Verdin	8 (11)	5 (13)	4.5 (5)	V
Cactus Wren	7 (10)	2 (5)	8 (8)	–
Canyon Wren	–	–	+ (+)	–
Rock Wren	–	–	+ (+)	–
Western Mockingbird	+ (–)	–	V	V
Palmer's Thrasher	6	1.5 (4)	2 (2)	V
Plumbeous Gnatcatcher	5 (7)	2.5 (6)	6 (6)	–
Phainopepla	6.5 (9)	4.5 (11)	.5 (1)	V
Son. White-rumped Shrike	V	.5 (1)	–	V
Lucy Warbler	–	V	–	–
Hooded Oriole	V	V	–	–
Dwarf Cowbird	V	V	–	–
Pyrrhuloxia	V	–	–	–
House Finch	7 (10)	1 (3)	2 (2)	–
Canyon Towhee	–	–	V	–
Desert Sparrow	+ (–)	+ (–)	+ (–)	V
Total Populations	64 (88)	42.5 (108)	35.5 (37)	0
Total Species	28	29	26	12

*Figures in parentheses indicate pairs per 100 acres while those species marked (V) are visitants.

TABLE 9. Migrant species showing periods recorded on the Inter-wash Areas (3 and 4).

Species	Date first recorded	Date last recorded	Total period recorded	Total number recorded
Violet-green Swallow	Feb. 27	March 20	24 days	9
Western Gnatcatcher	" 27	Feb. 27	1 "	1
Western Flycatcher	" 27	" 27	1 "	1
White-crowned Sparrow	March 7	April 21	45 "	24
Brewer's Sparrow	" 16	" 21	35 "	127
Cooper's Hawk	April 14	April 14	1 "	1
Western Tanager	May 3	May 3	1 "	2

Total migration period recorded - February 27 to May 3 - 68 days
Total number of migrating species - 7
Total number of migrating individuals - 165

ized the area proper for nesting and feeding purposes.

The dozen species observed in the creosote bush tract (Area 3) are doubtlessly breeding species nesting in the near vicinity and appeared on the area in search of food. It is generally known that extensive pure stands of creosote bush in the southwest deserts seldom attract many birds. However, when it occurs intermixed in or at the fringes of cacti, mesquite, and catclaw associations it has been observed that a number of birds make use of it (Anderson & Anderson 1946).

During the course of the study the nest sites of eight pairs of western red-tailed hawks, two pairs of Harris's hawks and two pairs of western horned owls were discovered. It is noteworthy that only two of the total nests observed were located outside of the "cruised area" although considerably more miles were covered in the remaining part of the Monument. The cruised area is a 5 by 15 mi. tract extending along the International Boundary Line which acts as its southern border. This tract embracing about 75 sq. mi. contained the nesting and hunting territories of ten pairs of the three species mentioned above, six of which were western red-tailed hawks and two each of Harris's hawks and western horned owls. Within the tract then each pair could control about 7.5 sq. mi. of hunting territory provided the niche requirements were similar. This figure appears to embrace considerable territory for a single species but, on occasion, members of the pairs of red-tailed hawks under observation were recorded at least three miles from their assumed nesting locality.

The greatest distance between two nests of the red-tailed hawk was approximately 6 mi. On the other hand only about 3 mi. separated the two closest nests. Considering only this species each pair could theoretically maintain a hunting territory of about 12.5 sq. mi.

THE COMPARATIVE POPULATIONS AND NESTING ACTIVITIES OF THE RESEARCH AREAS

COMPARATIVE POPULATION DENSITY

The monthly density of recorded individuals (Figure 4) presents a more graphic illustration of the

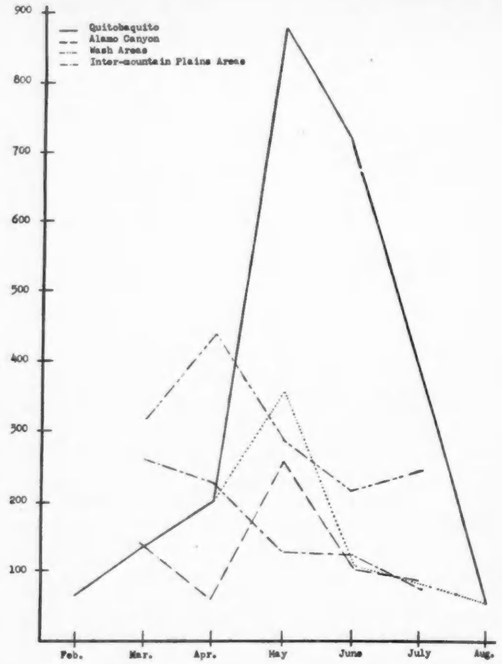

FIG. 4. Graph showing population density of individual birds on the study areas.

population distribution than is evident by the tables. As can be seen each study area presents a different population tendency.

From the data presented (Figs. 4 and 5) it appears that April and May are possibly the periods of peak migration through the areas, however, a more intensive analysis will introduce several other factors that have to be considered. The curve for Quitobaquito is greatly exaggerated during the months of May and June by the immense numbers of white-winged doves that frequented the place. If these individuals are subtracted (518 and 600, respectively) from the total number of individuals the curve approximates that of the other areas (Fig. 4). With 32 species recorded in May, this month appears to be the period of peak concentration at this area with April next. The heavy concentrations of white-winged doves are largely composed of transient individuals as well as a few early nesters in the vicinity. The first appearance of the species was on April 19 while the first active nest located was under construction on May 25. Following this a sudden splurge of nesting activity occurred. Neff (1940) noted that in 1939 the migration was normal with unusually heavy populations observed during late May and early June within the Arizona range of the species. By mid-June the summer population was distributed to the normal nesting grounds.

The wash areas (1 and 2) exhibited the next highest concentration of individuals. The peak popula-

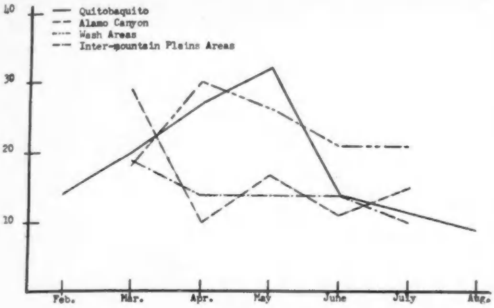

FIG. 5. Bird species density on the study areas.

tion density occurred during April and tapered off to a constant level by June. A total of 30 species, as compared to the 32 at Quitobaquito in the May peak, was recorded. Significantly, white-winged doves were in much lesser numbers in the washes preferring the vicinity of water sources and as a result did not greatly influence the population trend.

In the intermountain plains (Areas 3 and 4) the tendency was still somewhat different for the peak appeared in March, earlier than either of the areas discussed above. Congregations of white-crowned, Gambel's, and desert sparrows contributed heavily to the total numbers of individuals recorded. As would be expected the species tendency (Fig. 5) closely followed that of the total populations. Whether or not the earlier peak experienced here is due to the more open and therefore less attractive nature of the terrain, which would expose the birds to the elements, is suppositional but highly probable. Earlier seasonal movements through habitats of this nature may be customary before heat and water conditions became critical.

Most controversial is the picture portrayed by the population trend of the canyons. It is unlikely that two widely separated population peaks exist (March and May) as indicated in Figs. 4 and 5. It must be considered that the April figure is based on data from only one census and thereby is likely to introduce factors which might be changed by additional data. In view of the fact that the highest peak is in May it seems logical to assume that the same general tendency exists here that is apparent at Quitobaquito, namely that of a later peak population period than indicated by the remaining intermountain areas. This condition could be influenced by two primary factors: (1) sources of water are still present at this time in the canyons by virtue of numerous shaded tinajas, or pot-holes, in the rocks which have preserved remnants of the spring rains. As a result the need of additional water during the warm later seasons is not an inhibiting factor, and (2) sufficient shade and cover exists around permanent waterholes, such as Quitobaquito, and reaches a maximum in the more or less shaded mountain canyons. Thus shade, water, cover and food therefore are all available at these later dates.

On the basis of these data, then, the seasonal peaks of abundance for both numbers of individuals and of species during the current study were recorded in the following sequences: 1. March (open desert), 2. April (washes), and 3. May (mountain canyons and permanent water sources).

COMPARATIVE NESTING ACTIVITY

Active nests of 15 species of birds were located on the research areas that were intensively studied. Extreme nesting dates recorded were March 6 (Palmer's thrasher nest containing eggs) and July 27, when nests of both the Palmer's thrasher and white-winged dove were found with fresh eggs. The approximate total nesting season then extended at least from about February 28 to August 15. The final censuses were conducted on July 27 and 28. The Palmer's thrasher exhibited the most prolonged nesting period of all the species under observation for approximately 170 days (February 28-August 15) of nesting activity were recorded for the species. In contrast the total period of nesting activity for the one pair of Sonoran white-rumped shrikes amounted to only about 35 days.

The nesting components are predominately composed of permanent residents which are represented by ten species while the summer residents number only five species. As a rule the first mentioned group appear to be the earlier nesters, for seven of the ten species listed were actively nesting by March. The three exceptions (gila woodpecker, ash-throated flycatcher, and Sonoran white-rumped shrike) delayed until April. Only one species of the summer residents, phainopepla, was recorded actively nesting in March. Western mourning doves had started nests by the middle of April while the remaining three species delayed until May before commencing nest operations.

Eight of the tabulated species apparently raised two broods during the breeding season. Of these only the three species of doves (white-winged, mourning, and Mexican ground doves) are summer residents. The remaining five species are permanent residents. The species rearing two broods are: western mourning dove, white-winged dove, Mexican ground dove, gila woodpecker, verdin, cactus wren, Palmer's thrasher, and house finch.

COMPARISON WITH SIMILAR DESERT BIRD POPULATION STUDIES

Two breeding bird population studies were conducted by Hutchinson & Hutchinson (1941, 1942) in the Colorado Desert of California. Being in the western aspect of the Sonoran desert these studies provide a direct and interesting correlation with the breeding birds found in the Arizona aspect as determined in the intermountain study areas of the current project. This desert area encompassed 37 ac. of typical Colorado desert. Creosote bush, desert lavender (*Hyptis emoryi*), burrow-weed, (*Franseria dumosa*), Encelia (*Encelia farinosa*), cat's claw and buckthorn cholla (*Opuntia acanthocarpa*) were the

predominant plant species sparsely scattered on sandy gravel strewn with rocks. Along a stream that crossed the area the vegetation was dense and high with the mesquite forming impenetrable thickets in some cases. These plant species are prominent constituents of the flora in the study areas established during the current study (Table 3).

Table 10 lists the species and comparative densities of the breeding populations for the two areas. The Colorado desert areas were censused during two consecutive breeding seasons by the same workers. A total of 26 breeding species was recorded during the three seasons on the two areas mentioned, of which ten were common to both (Table 10). For comparative purposes data from the four intermountain plains areas (Areas 1, 2, 3 and 4) were combined to present the same wash and hinterland

TABLE 10. Comparison of the breeding bird density (pairs per 100 ac.) of two areas in the Colorado and Arizona sub-divisions of the Sonoran Desert.

Species	COLORADO DESERT (37 acres)		Arizona Desert (210 acres)
	1941	1942	1949
Gambel's Quail	3	3	6
Phainopepla	3	3	6
Red-shafted Flicker	3	—	—
Costa's Hummingbird	35	38	+
Dwarf Cowbird	3	—	—
Desert Sparrow	16	16	+
Cactus Wren	3	11	8
Arizona Verdin	14	8	9
Sonora Gnatcatcher	8	16	7
Abert's Towhee	3	—	—
Rock Wren	5	8	+
Western Mourning Dove	—	3	2
Black Phoebe	—	3	—
Bewicks Wren	—	5	—
House Finch	—	5	5
Green-backed Goldfinch	—	5	—
California Towhee	—	3	—
White-winged Dove	—	—	13
Palmer's Thrasher	—	—	5
Gila Woodpecker	—	—	3
Arizona Crested Flycatcher	—	—	3
Ferruginous Pygmy Owl	—	—	.5
Sparrow Hawk	—	—	.5
Ash-throated Flycatcher	—	—	1
Sonoran White-rumped Shrike	—	—	.5
Mexican Ground Dove	—	—	.5
Total number of species	11	14	16
Breeding density per 100 acres	96	127	70

conditions as did the California study. The breeding density per 100 ac. is relatively consistent during the three seasons represented with the slightly higher figures for the Colorado desert areas being due in large part to the high concentration of the Costa's hummingbird. The number of species recorded on the two areas during the seasons studied is also remarkably constant.

The species composition and densities of the non-breeding birds recorded on these two areas are tabulated in Table 11. Transients, wintering residents still lingering in the areas, unmated males, and casual visitors comprised this category. As indicated in the table (11) the final density of individuals (breeding plus non-breeding) is also slightly less than that recorded in both the breeding and non-breeding categories in the California study and could feasibly be due to the presence of the stream running through the area. It is not recorded as to whether the stream contained water or was a dry arroyo, as was the case in the Arizona study plots. The presence of water would undoubtedly account for large numbers of individuals such as the Costa's hummingbird.

In an analysis of the ecological components of the northern desert shrub biome in western Utah, Fautin (1946) noted that the bird populations in all communities were relatively low. From actual counts of 4 hectare (10 ac.) plots, the average summer populations varied from 10.6 / 10 hectares (25 ac.) in the shadscale, *Atriplex confertifolla,* 12.6 in the tetradymia, *Tetradymia glabrata,* to 27.0 in the greasewood, *Sarcobatus vermiculatus,* communities. In terms of individuals per 100 ac. these figures are 42.4, 50.4 and 108 respectively. Populations were greatest in the tetradymia and shadscale communities during spring and early summer.

FAMILY ORIGINS OF THE BREEDING SPECIES

An analysis of the zoogeographic origin of the populations indicate a difference between those of the Arizona desert plains and those of the Colorado desert (Table 12). The region of origin for the various groups is taken from Mayr (1946) and for most species is based on the origin of the family, except in the Fringillidae where the sub-families are used. In some cases the genus is considered. Due to the fact that the analysis by pairs is based only on the birds as found on specific community censuses while the analysis by species includes all the breeding

TABLE 11. Comparison of the non-breeding bird densities of two areas in the Colorado and Arizona sub-division of the Sonoran Desert, including final density of the total avian population.

Areas	No. of censuses taken	Total no. species recorded	Total no. individuals recorded	Ave. no. recorded per census	No. of breeding individuals	Final density (per 100 ac.)
Colorado Desert (1941)	17	37	149	8.7	190	199
Colorado Desert (1942)	—	—	—	20.6	248	269
Arizona Desert (1949)	71	21	460	6.5	138	145

TABLE 12. Zoogeographic origin of the breeding birds in two southwestern desert areas.

Areas	South American		North American		Old World		Unanalyzed	
	Species	Pairs	Species	Pairs	Species	Pairs	Species	Pairs
Colorado Desert (California)	11.1	37.1	77.8	48.6	11.1	14.3	—	—
Arizona Desert (OPCNM)	21.6	6.1	35	53.0	26.7	39.4	16.6	—

species occurring on the Monument, the data are, therefore, not entirely comparable.

Considering first the species analysis as listed in Table 12 it is apparent that the North American element is, by far, the more important in so far as the two desert areas are concerned. The considerably higher figure listed for the Colorado desert is due to the fact that seven of the nine families represented are of North American origin. In the Arizona area only 11 of 60 families come in this category. Had a larger area been studied in the former region where more species would likely have been encountered these figures would no doubt be more comparable.

The South American and Old World categories apparently are about equally represented in the Colorado region while in the Arizona study the latter center of origin presents a slighly larger percentage of species and pairs than does the South American.

The families Trochillidae, Tyrannidae, and Icteridae, which Mayr lists as belonging to the Pan-American element but probably originally South American, are included under the latter category herein.

Comparison of the pairs analysis presents some interesting observations. In the Old World element, the same general tendency as the species is expressed. On the other hand the reverse situation occurs in the South American element for the pairs analysis as is expected by the expressed species tendency. The large percentage of pairs in this category recorded in the California region is due to the large density of breeding Costa's hummingbird, the single family of South American origin. Thirty-seven per cent of the breeding pairs were members of this species, for 13 nests were located of the total 35 breeding pairs of birds recorded.

HABITAT NICHES OCCUPIED BY THE BREEDING SPECIES

Contrary to many popular opinions desert habitats are varied and numerous. There is as much difference between habitats in the desert as in any other region and the relative sharpness of demarcation forms one of the most striking and characteristic features of arid regions (Spaulding 1909).

Turnage (1939) in his analysis of desert subsoil temperatures notes that the minimum temperature periods at three depths (3, 6, and 12 ft.) occurred just before and during the spring growing season when leaf and stem growth of plants was rather active. Maximum temperature periods came during the summer rainy season when plant growth was at a maximum.

Gambel's quail, the only ground nesting species recorded on the reseach areas brought off young during the month of May with the first brood of very young chicks observed on May 12. Such species as Palmer's thrasher, verdin, and Sonora gnatcatcher who nest above the soil surface where air currents have a moderating effect on the temperature may extend the nesting season into July when temperatures are much higher.

Different types of nests are utilized as well as choice of location by many species. On the three study areas (1, 2, and 3) four nest types were apparent, namely; (a) the conventional open-top form of the house finch, phainopepla, Palmer's thrasher, Sonora gnatcatcher, white-rumped shrike, red-tailed hawk, and western horned owl, (b) close-roofed nests of the cactus wren and verdin, (c) platform nests built by the Mexican ground, white-winged, and western mourning doves, and (d) hole nests in saguaros, built by the gila woodpecker, and utilized by the Arizona crested and ash-throated flycatchers after abandonment by the woodpeckers.

Temperatures were taken in 13 nests of four species of birds included in the first two categories above (Table 13). The nest temperatures were determined by inserting a small thermometer into the nest chamber and checked after a suitable time had elapsed. As a rule, the two species building covered nests, cactus wren and verdin, had nest temperatures slightly lower than those found in the open-topped structures of the phainopepla and Sonora gnatcatcher. However, they were inclined to place them in more exposed situations and thus were subjected to greater temperatures. That is particularly true of the cactus wren which frequents the exposed interwash areas

TABLE 13. Nest environment data for four species of desert birds.

Species	Plant utilized	Height from ground (in.)	Exposure	Nest temperature in degrees F.
Cactus Wren	Cholla	60	SW	76
" "	Cholla	63	E	88
" "	Cholla	66	N	94
Verdin	Palo verde	56	W	81
"	Condalia	64	E	92
"	Cholla	70	E	94
"	Condalia	100	W	102
"	Condalia	64	E	98
"	Palo verde	65	N	101
Phainopepla	Palo verde	72	N	98
"	Catclaw	50	E	98
"	Palo verde	72	W	90
Sonora Gnatcatcher	Condalia	55	Center	94

and nests primarily in the chain cholla. Although well protected nest sites may be available in these plants this species is in direct competition for them with the larger, more aggressive Palmer's thrasher which also inhabits the same upland situations. Huey (1942) states: "their choice habitat amongst the chollas cactus was occupied commonly by Palmer's thrashers and the competition appeared to be too much for the wrens." As a result the denser more luxuriant chollas were usually taken by the thrashers which needed considerable protection for their open nests. Verdin nests, usually placed on the periphery of the tree or cholla, and varying in height from 3-20 ft., were commonly fully exposed but, as was the case with the cactus wren, always kept the nest in full repair at all seasons.

The species building open-topped nests, on the other hand, placed them in well protected spots usually or where circulation of cooling breezes occurred. The Sonora gnatcatcher invariably used dense condalia or other shrubs as nest sites and located the structure deep within the interior of the plant. Those species included under group (c) above (the three dove species) usually placed their sparsely constructed nests on the horizontal branches in such trees as the palo verde, ironwood, and condalia. One white-winged dove nest was placed on a broken vertical stump of a saguaro which was fully exposed to the June sun. The pair of Mexican ground doves built a nest on a slanting, almost horizontal trunk of a dead ironwood five feet above the ground. This site, used for successfully rearing two broods of young, was also fully exposed to the sun.

The hole-nesting species and the larger birds of prey, whose nests were all located in saguaros were apparently less affected by the temperatures than were the other species concerned. The red-tailed and Harris's hawk, as well as the western horned owls, commenced nesting activities well in advance of most of the other species and had young fledged or well developed by the time extreme temperatures occurred.

Locations of the nests varied with the availability of suitable sites. The higher nesting species such as the three birds of prey, the two flycatchers, and the gila woodpecker utilized the saguaro extensively, with the ash-throated and Arizona crested flycatchers being dependent upon the abandoned nesting cavities of the gila woodpecker in large part. The two hawk species (red-tailed and Harris's) usually placed their nests in the giant cactus on specimens where supporting arms were noticeably higher than the surrounding plants. The white-winged and western mourning dove, and the phainopepla utilized the higher wash plants as the condalia, mesquite and ironwood trees, for the most part, and exhibited a wide range of nest heights as a result. Conversely, those birds which preferred the cholla cactus (cactus wren, Palmer's thrasher, house finch) were necessarily content with little height variation but had the excellent protection of the spiny branches which surrounded the nest. The relatively low nesting verdin utilized both the cholla and several plant species along the washes. In turn the cleverly constructed nests, without fail, always had several spiny catclaw twigs incorporated around the entrance hole and often formed a short protecting porch-like projection over the entrance with this same material. As a result, even though the nest was rather low and placed in an open-branched wash tree it presented quite a challenge to most predators. Only one nest of the desert sparrow was found (Alamo Canyon) and was located in the interior of a thick bushy bur sage. Completely invisible from all sides of the nest plant, it was discovered only by the actions of the adults and the presence of a fledgling in a neighboring shrub.

Ground nesting species are not so common in such areas where the sparsely scattered bushes afford little cover. Only in the vicinity of water holes and along the more thickly vegetated washes, with the exception of the canyons, does the ground cover afford suitable nesting niches. Only a single nest of the Gambel's quail was located during the study. The nest site was under a thick two-foot high bur sage along the south periphery of a large condalia tree at Agua Jita. In the case of the turkey vultures, however, vegetative cover was not a contributing factor to nesting success. The one nest found of this species, was situated in the center of a large rock pile on the open desert. The boulders were so arranged as to form a cairn with a single small opening into a sizeable room within the pile. The entrance was just large enough to permit the birds to enter into the nesting cavity which was some 10 ft. in diameter and 3.5 ft. high.

PLANT UTILIZATION AS RELATED TO THE FOOD, WATER AND NESTING REQUIREMENTS

Water requirements of desert animals have long been a subject of interest to many scientists. Most work to date has been concerned with desert mammals. Bailey (1923), Sumner (1925), and Vorhies (1928, 1945) have made outstanding contributions to our scant knowledge of the water problem of these animals thriving in arid regions. The problem has been considered in the old world deserts by Buxton (1923) and Feniuk & Kazantzera (1937).

Animals living in desert country are commonly thought to derive moisture from two chief sources when free water is not available. These are succulent foods and metabolic processes. Many mammals have been successfully kept in captivity for months, even years, subsisting on diets of air dried foods as rolled oats and dry grain.

Table 14 indicates some common sources of food and water. As a result, the critical hot summer seasons. Throughout the nesting period various plants are producing flowers, which attract large numbers of insects, or fruits which supply both food and water. As a result, the critical hot summer months are endured with relative ease by most of

TABLE 14. Approximate seasons of common food and water sources available to the desert fauna during the current study (1949).

Source	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Precipitation	XXXX						XX	XX	XX	XXXX		XXXX
Winter Annuals	XX										XX	XXXX
Spring Annuals			XXXX	XX								
Mesquite (*Prosopis juliflora*)			XX	XXXX	XXXX	XXXX	XXXX	XX				
Mistletoe (*Phoradendron californicum*)				XXXX	XXXX							
Hedgehog Cactus (*Echinocereus*)				XX	XXXX	XX						
Indian Wheat (*Plantago*)				XX	XXXX	XXX						
Condalia (*Condalia lycioides*)				XX	XXXX	XXXX						
Saguaro (*Cereus giganteus*)				X	XXXX	XXXX	XXXX					
Lycium (*Lycium berlandieri*)					XXXX							
Catclaw (*Acacia greggii*)					XXXX	XXXX	XXXX	X				
Organ Pipe Cactus (*Cereus thurberi*)					XXXX	XXXX	XXXX	XX				
Prickly Pear Cactus (*Opuntia engelmanii*)					XXXX	XXXX	XXXX	XXX				
Ironwood (*Olneya tesota*)					XX	XXXX	XXXX	X				
Palo verde (*Circidium*)						XXXX						
Barrel Cactus (*Echinocactus*)							XX	XXXX	XXX			
Hackberry (*Celtis reticulata*)						XXXX			XXXX			

the birds. Only the permanent residents and winter visitants would seemingly have the most difficulty and that would be during the cooler winter season. Rains occurred in September, October, December, and January which alleviated most of the water difficulty, temporarily, for it is not so important during this period of cooler weather and higher humidity (Table 14). Invertebrates, seeds, winter buds, and other foods are available most of this time, and even these groups experience few unfavorable periods.

An examination of the winter and permanent residents will reveal the following four food-preference categories of birds: (a) Carnivorous, 19%; (b) Insectivorous, 43%; (c) Seed eaters, 30%; (d) and Miscellaneous, 8%.

(a) *Carnivorous species.* Rodents and smaller birds play the predominant role in the food habits of hawks and owls and are available the year around. Least difficulty for survival should be experienced by these birds.

(b) *Insectivorous species.* Sixteen species are listed as primarily insectivorous. These include the gnatcatchers, shrikes, vireos, flycatchers, wrens, thrashers, woodpeckers, phainopepla, and verdin. The food habits of these species vary with the seasons and during the summer when the mistletoe is in fruit it comprises almost 100% of the food of the phainopepla. Cactus wrens and Palmer's thrashers were often seen pecking at the unopen fruits of the saguaro to get at the seeds and sweet juicy pulp within. The woodpeckers were somewhat independent of the surrounding conditions for water was accessible to them by merely piercing the tough outer covering of the saguaro which exposed the watery pulp beneath. This trait undoubtedy benefited other species seeking water for considerable time may elapse before the juices hardened to seal the wound from further water loss. One instance of this procedure was recorded on March 16. A gila woodpecker was observed pecking on the extreme top of an 18 ft. saguaro. The purpose of his efforts was unknown but evidently the outer covering of the plant was pierced for chips could be seen falling to the ground. After working for some 15 min. the woodpecker departed and his place was soon taken by a Palmer's thrasher who discovered the wound and commenced picking at the spot, accompanied by an occasional raising of the head in the characteristic fashion of a drinking bird. After satisfying his thirst the thrasher departed and in turn the spot was utilized by one of a pair of cactus wrens that was building nearby. The purpose of the wren's visit was apparently to sing from the elevated perch for several minutes of singing were concluded before this bird also was noticed picking and drinking from the same spot.

Insects are apparently abundant during the winter season, as well, for Huey (1942) observed hundreds of white-throated swifts capturing insects that had been carried up from Alamo Canyon by an updraught of wind during his study in the canyon on December 14.

(c) *Seed eaters.* This group is composed mostly of Fringillids, with the exception the Gambel's quail. Food is obtained during the winter seasons from the many minor plant species as well as mesquite and other seed bearing trees. Insects are no doubt utilized as well when they are chanced upon. Gambel's quail uses both vegetable and animal foods depending on the season. Vegetable food reaches its maximum in

February, its minimum in June, at which time animal matter reaches its peak (Gorsuch 1934). Mesquite far surpasses any other species in both frequency of occurrence and quantity and furnishes food throughout the year. Large quantities of buds and flowers are taken in the spring by many species of birds while during the fall and winter the seeds are eaten in vast numbers. Most small birds cannot break the hard tough pod of the mesquite but many become available after coyotes, cattle, and other animals have eaten pods which are digested and the beans passed out entirely and thus made available to quail and other species. Various cacti furnish a constant source of food to most species of wildlife on the desert. Gorsuch (1934) mentions that during the hot dry season it is not uncommon to find quail with beaks and faces stained a deep red from the juices of the prickly pear fruits upon which they have been gorging. Cholla fruits are apparently less attractive to the quail but the seeds are readily utilized as recorded by the above writer. New leaves of the composites (Compositae) are taken during winter months while budding flowers are eaten in the spring.

The desert hackberry serves a dual purpose of both food and cover and is one of the prime importance to quail according to Gorsuch. The orange-colored berries are produced from mid-summer through the fall months and are greatly relished by birds.

(d) *Miscellaneous species.* Three species include the killdeer, roadrunner, and raven. In the case of the killdeer, food and water are no problem for it is restricted to permanent water sites where these natural requirements are abundant.

Especial mention should be made of the importance of the saguaro in its effect on the desert wildlife. Utilized by a majority of the mammal and bird species it is one of the most important components of the desert flora, ranking high with such plants as mesquite and hackberry. The flowers appearing in April are a source of both food and water for the bird species. The large flowers have the typical waxy gloss of the cactus blossoms and are persistent for a few days even during the hot seasons. Having a deep bell-shaped form the numerous yellow stamens completely cover the slightly elongated hypanthium which is filled with a sweet thick nectar. Many observations were made of birds digging deep into these flowers for the insects and apparently to sip the juice. The doves, both white-winged and western mourning, were exceptionally fond of this source of nourishment.

It is probable that the presence of the larger numbers of saguaros on Area 2 partly accounted for the considerably higher dove populations which occurred there. By counting the total number of individual saguaros present, it was found that 638 (15.8 / ac.) mature, producing plants were found in Area 2 as contrasted to 261 (3.7 / ac.) in the other area. Expressing these data in terms of percentages in Area 2, 118% more saguaros were present, 23% more birds of all species comprised the population and a difference of 215% more doves were recorded in the same area.

By crudely weighing several lots of saguaro fruits an average of approximately one ounce of juicy pulp was found to be available in each fruit. Being rather tender when ripening and finally popping open at maturity those fruits were available to the birds and scores were knocked off the plants to be eaten by cattle, deer, coyotes, and myriads of other desert animals. Up to a hundred blossoms have been counted on a single young plant while four or five arms, each producing blossoms and fruits, are found on many saguaros. As a result, a tremendous amount of food and juice is available during the hot critical summer period when this plant is bearing.

An interesting correlation may be drawn between the flowering of the saguaro and the presence of the white-winged dove. The date of the first dove recorded on the Monument was April 19 and two days later (April 21), the first saguaro blossom was seen. The breeding period of this species and the flowering and fruiting season of the saguaro both occur from April to August, approximately. Wetmore (1920) stated that the favorite food of the white-wings along the Gila River during the summer period was the purple drupe borne by *Condalia spatulata* and the fruits of the giant cactus, which they ate as rapidly as they ripened. Gilman (1911) noted that their coming was coincident with the ripening of the berries of the wild jujube, *Zizyphus lycioides*, upon which they fed greedily as long as the fruit lasted, consuming both ripe and green. Gilman adds that the giant cactus furnishes them (white-winged doves) a large amount of food and noted that: "They may be seen on top of the giant columns as soon as the first blossoms appear, thrusting their bills into the trumpet-shaped flowers, but whether for insects, pollen, or nectar was not learned. As soon as the fruit ripens, however, there is no doubt as to what they are seeking. Their actions are a sufficient index even without the telltale red stain around their mouths. They frequent the cactus groves as long as any fruit is left, flying a long distance to reach this delicacy."

Anderson & Anderson (1946) recorded, near Tucson, instances of English sparrows (*Passer domesticus*) eating the buds of the creosote bush and house finches crushing the fuzzy fruits with their bills to get at the seeds inside. Another instance of the green-backed goldfinch (*Spinus psaltria*) sampling the fruit was also made. Although the creosote bush fruits ripen in enormous numbers each year, and are easily accessible, none of the desert birds apparently feeds on them regularly. Only one observation of a bird feeding from this species was made during the current study, that being a cactus wren which may have been eating the flowers or more likely snaring insects from the blossoms.

An attempt was made to determine what plants were commonly utilized in the nest construction of the various species of birds. One verdin nest was

completely analyzed as to plant species involved and produced some interesting facts of construction and utilization of various plant twigs. The globular structure had a depth and breadth of about nine by seven in. while the nesting cavity measured about five by three in. The nest was divided into three distinct layers (1) an outer rough layer of larger twigs which made up about 25% of the bulk, (2) a middle layer comprising most of the structure (70%) and made of short twigs and leaves of softer composition, and (3) an inner layer of feathers which made up the remaining 5% of the total bulk.

(1). This layer was composed of five species of plants: Lycium, 45%; ironwood, 21%; hackberry, 14%; Condalia, 4% and Acacia 1%. A remaining 15% was unidentified. The catclaw was represented by the lowest per cent of occurrence (1%) but also the twigs were strategically placed over the entrance hole. A count of 40 twigs revealed an average of 3.8 in. in length, the longest and shortest being 7 and 1 in., respectively.

(2). The middle layer was chiefly made up of shorter finer twigs of the species listed above, with the exception of the catclaw. No thorns were found here. A considerable proportion of leaves were added in this layer to provide insulation and softness to the chamber. These were principally ironwood and mesquite.

(3). The lining of the nesting chamber proper was made completely of feathers, all of small size and of undetermined origin. Breast feathers of the cactus wren and Gambel's quail were most common.

TERRITORIAL BEHAVIOR AND NESTING ACTIVITY OF THE BREEDING SPECIES

COMPARATIVE SIZES OF THE TERRITORIES

During the current study a more or less consistent size of territories was evident, particularly in the wash areas, where the habitats of both plots were similar, regardless of the population density. In Area 1 twice the number of Gambel's quail was present than were in Area 2 yet the average nesting territorial sizes were surprisingly similar (Table 15). Other species (gila woodpecker, verdin, Palmer's thrasher, Sonora gnatcatcher) exhibited the same tendency. On the other hand, where the same number of birds was present on each area the sizes of the territories may vary, such as shown by the phainopepla and Arizona crested flycatcher. The one pair of cactus wrens nesting in Area 2 maintained a considerably larger territory than those of the first wash plot.

Comparison of these wash territory sizes, however, to the open desert typified by Area 3 reveals quite a different tendency. Here all of the average territory sizes are larger than those maintained by the same species in the wash situation. Extreme cases are provided by four species; the gila woodpecker, ash-throated flycatcher, Palmer's thrasher, and phainopepla (Table 15). Every species, with the exception of the cactus wren, at least doubled their territory sizes. In the case of the exception cited, it is interesting to note that the seven open desert territories averaged less than an ac. (.7) larger than the single territory maintained by the species in Area 2. Perhaps these sizes recorded may be the optimum desired under unmolested and uncrowded conditions. Also the presence of a richer food supply along the washes might have accounted for the smaller territories in those areas. In the open desert area a considerable amount of additional suitable habitat was available had the individuals desired to extend their territories.

Both the ferruginous pygmy owl and sparrow hawk maintained a hunting territory over Area 1 and the portions in which they were observed were plotted mostly along the wash. The hunting territory of each was determined and listed in the table. Young of the owl species were recorded on several occasions along the wash. Two mockingbirds established territories but so far as could be ascertained, these males did not mate. One male maintained his territory from March 8 to April 25 and the other remained from March 19 to April 25. No evidence of territorial

TABLE 15. Comparative territorial sizes (in acres) for the common nesting species on the three study areas.

Species	AREA 1				AREA 2				AREA 3			
	Number of territories	Max.	Min.	Ave.	Number of territories	Max.	Min.	Ave.	Number of territories	Max.	Min.	Ave.
Cactus Wren	7	6.3	3.1	4.6	1	–	–	8.9	7	13.0	6.6	9.6
Gambel's Quail	6	4.5	1.7	3.4	3	3.8	3.2	3.1	+	+	+	+
Verdin	6	1.9	1.0	1.3	4	1.7	.9	1.3	4	6.6	5.2	5.7
Phainopepla	5	3.1	1.7	2.4	5	1.9	1.2	1.4	1	–	–	10.5
Sonora Gnatcatcher	4	2.6	2.0	2.4	2	2.3	2.3	2.3	6	6.6	4.2	5.2
Palmer's Thrasher	3	11.5	9.9	10.5	1	–	–	9.2	2	48.3	29.4	38.9
Gila Woodpecker	2	11.6	11.3	11.5	1	–	–	11.0	2	24.7	24.1	24.4
Arizona Crested Flycatcher	2	12.7	9.4	11.0	2	10.4	6.3	8.4	2	20.9	18.8	19.9
Western Mockingbird	2	8.2	7.1	7.7	–	–	–	–	–	–	–	–
Ash-throated Flycatcher	1	–	–	7.3	+	+	+	+	1	–	–	24.7
Ferruginous Pygmy Owl	1	–	–	20.8	–	–	–	–	–	–	–	–
Sparrow Hawk	1	–	–	22.6	–	–	–	–	–	–	–	–
House Finch	+	+	+	+	+	+	+	+	+	–	–	8.2

behavior was noted for any of the pairs of house finches recorded in Area 1. Active nests were sometimes within 100 ft. of each other and no competition was evident. The one pair of this species nesting in Area 3 was recorded during the period of nesting over an area embracing some 8.2 ac.

No territorial behavior was noted for either of the common breeding dove species.

NESTING SUCCESS OF THE BREEDING SPECIES

Considering first the larger common birds of prey 100% nest success was recorded for eight nests of the western red-tailed hawk that were observed. Five of the eight nests contained two eggs each while the remainder had three each. One of the two nests located of the Harris's hawk did not produce its full clutch. In this case one of the two day-old young was either pushed or fell from the nest and was found dead at the base of the saguaro that provided the nest-site. The other nest contained three eggs. For the two hawk species listed all the eggs hatched that were laid. In the case of the western horned owl, the sizes of the original clutches were not known, however, both the nests located were found while the young were quite undeveloped and it is reasonable to assume that if a mate had been present it would not have fledged prior to the discovery of the nest-site. Bent (1938) states that two eggs form a set and sometimes three may be found.

A more significant appraisal of the nesting success can be derived from Table 16 where the data are presented in terms of percentages. The two dove species which are common nesters, build the typical flat platform type of nest and are not so particular concerning the exposure of the nest site. As a result they exhibit the lowest per cent of nesting success of any of the species studied. The period of greatest mortality appeared to be during the incubation phase. In a study of 56 white-winged dove nests in a southern Arizona survey, Arnold (1943) recorded a 75% success in 1942. The same area, according to Arnold, produced a 53% success in 1941. This figure was compiled on the basis of 60 nests. The 1941 figure did not include the probably more successful early season nests.

It is interesting to note the close similarity in the per cent of successful nests of the cactus wren, verdin, Palmer's thrasher, and house finch. With the exception of the verdin, all utilized chollas exclusively as nesting sites. Palo verde trees were used most frequently (7 out of 15) by verdins.

In the Tuscon Mountain Park area Arnold (1943) found that birds (white-winged doves) nesting in low open sites on cholla cactus have a high percentage of success. The current study seems to bear out this observation for species other than the doves mentioned above.

As a whole, 70% of the total number of active nests were successful, fledging at least one young. Table 16 lists the hatching and fledging data for these successful nests thereby providing an index to the fertility and viability of the eggs, as well as to the rearing efficiency of the adults.

A total of 30 nests failed to produce fledglings successfully on the study areas. The factors apparently responsible for the unsuccessfulness of the attempts are summarized in Table 17. Six nests were raided during the egg stage. In all cases the nests appeared to be undisturbed with only the eggs missing. In one instance noted both eggs of the phainopepla nest were punctured. A Sonora gnatcatcher was surprised at or near the nest on the observers' approach and rapidly flew from the vicinity.

A known cause for desertion by incubating house finches was due to parasitization by the dwarf cowbird. A pair of white-winged doves deserted their nest after the eggs were punctured similarly to those of the phainopeplas mentioned above.

TABLE 16. Nesting success of the common species of birds on three Lower Sonoran Desert areas.

Species	Total no. nest active	Total no. eggs laid	% eggs laid that hatched	% young hatched that fledged	% eggs laid that fledged	% nest with at least one young fledged	No. eggs laid in successful nests	% eggs hatched in successful nests	% eggs hatched that fledged in successful nests
White-winged Dove	24	44	45	90	41	42	18	100	100
Cactus Wren	20	69	86	97	83	80	56	100	100
Verdin	15	56	96	85	82	80	48	96	100
Palmer's Thrasher	15	40	92	78	72	80	31	97	97
House Finch	10	41	80	100	80	80	33	100	100
Phainopepla	8	18	78	93	72	75	14	100	93
W. Mourning Dove	4	8	50	100	50	50	4	100	100
Mexican Ground Dove	2	4	100	100	100	100	4	100	100
W. Red-tailed Hawk	1	2	100	100	100	100	2	100	100
W. Horned Owl	1	1	100	100	100	100	1	100	100
Son. White-rumped Shrike	1	6	100	100	100	100	6	100	100
Sonora Gnatcatcher	1	5	20	100	20	100	5	40	50
Fledged broods seen	(5)	—	—	—	—	—	—	—	—
Gambel Quail	—	—	—	—	—	—	—	—	—
Fledged broods seen	(6)	—	—	—	—	—	—	—	—
Totals	102	294	81	91	72	70	222	97	99

TABLE 17. Factors responsible for nest losses on the three study areas.

Species	No. nests unsuccessful	RAIDED		ABANDONED		Nest tipped	Undetermined
		egg stage	nestling stage	egg stage	nestling stage		
White-winged Dove	14	3	1	2	..	..	8
Cactus Wren	4	..	3	..	1		
Verdin	3	..	1	1	1		
Palmer's Thrasher	3	1	1	..	..	1	
House Finch	2	..	..	2			
Phainopepla	2	1	..	1			
Western Mourning Dove	2	1	1				
Totals	30	6	7	6	2	1	8

Two cases are listed of birds deserting the nest with young still unfledged. A cactus wren nest was checked on April 25 at which time the young were vigorous and just commencing to develop pin feathers. Five days later all three young were dead and completely dehydrated. The pin feathers were well developed at the time of death. No evidence of parasites was present and adult birds were in the area. Factors causing the deaths of the fledglings are undetermined. The other case was of a similar nature involving a nest of verdins. This nest was placed about $2\frac{1}{2}$ ft. up in a cholla and was found on April 5 with four eggs. By April 21 all were dead and completely dehydrated. The adults were not in the vicinity. No traces of tracks were visible beneath the nest nor was the structure itself damaged. No parasites were found on the young or in the nest. It is known that direct rays of a bright sun can readily have a disastrous effect upon nestlings within a few minutes (Willford 1925) and perhaps could feasibly have raised the temperature within such closed structures, under certain conditions, to a lethal threshold. However, it seems more likely that either parasites or the death of the adults was the responsible factor.

One nest of the Palmer's thrasher was the victim of strong winds which so loosened its attachments that it tipped over, spilling the fully feathered young into the chollas. Two of the three fledglings were impaled on the thorns of the cactus while the third was missing. Both were dehydrated.

Several factors may be attributed to the large number of raided nests. In addition to the egg puncturing, probably by some bird, the area abounds with predators, as the coyote, ground squirrels, bobcat, birds of prey, and several species of snakes that no doubt take their toll of nestlings and eggs. One white-winged dove nest was unquestionably destroyed by a coyote who consumed both the eggs and the incubating bird. A few scattered feathers were found on the ground as well as several distinct tracks of the predator. The nest was about five feet high in an acacia, growing along the wash in Area 1. On one occasion, a gray-tailed antelope ground squirrel (*Citellus h. harrisii*) was found in an old nest of the Palmer's thrasher which was placed up in a cholla. As to their ability to negotiate the hazardous chollas Huey (1942) states: "At times they were seen atop bristling-spined cholla cactus, where they sat erect to view the surrounding area. How they could negotiate the climb over the vicious thorns was always a question, for the soft pads of the feet on specimens taken in such positions never contained spines nor were there scars to indicate former difficulties."

On July 28, a large Arizona bull snake (*Pituophis sayi affinis*) was discovered 4 ft. up in a large ironwood tree in Area 2. Although the tree contained no active nest, so far as was known, the presence of this potential enemy had aroused a good number of birds. Eleven individuals of six species were present in the tree: three verdins, one white-winged dove, two Sonora gnatcatchers, two cactus wrens, two gila woodpeckers, and a Scott's oriole. Instances of eggs failing to hatch were recorded on four occasions. In two cases one egg of the clutch failed to hatch in verdin's nests and a pair of Palmer's thrashers fledged two young while leaving an egg in the nest. The Sonora gnatcatcher, already mentioned, was the remaining species who failed to hatch the complete clutch for only two of the five eggs hatched and only one of these fledged.

Young birds sometimes experienced considerable difficulty with the thorns of the cholla. On April 30, the nest of a Palmer's thrasher was found with a fully feathered young bird perched on the rim of the structure with one wing firmly held by the thorns. The bird was dead, being completely dehydrated, while the nest contained two eggs of the second brood. The incubating bird was flushed from the nest. Similar instances of young birds jumping from the nest during advanced nestling stages and becoming entangled with the thorns were recorded. Twice the fledglings became so securely fastened that only after considerable effort, were they freed by the writer.

SUMMARY AND CONCLUSIONS

Four areas exhibiting typical lower Sonoran desert vegetation were intensively studied in Organ Pipe Cactus National Monument, Arizona, during June and July of 1948 and from February through August 1949. Of these, two represented wash situations

and two were located in the intermountain plains. A total of 398 species of plants were recorded on the Monument. Many represent new locality records and include range extensions of considerable distances.

Two major eco-systems are found in the Monument being (1) the alluvial fill of the intermountain valley regions and (2) the mountain lava-granite complex.

By means of plot, transect, and continuous line counts of the wash plants, the plant species composition and relative abundance of each species was determined. The wash plots were predominately tree areas with mesquite, palo verde, ironwood, and saguaros particularly abundant. Another area was typical open desert with creosote bush, bur sages, chain cholla, and palo verde trees most common while another was 100% creosote bush.

Censusing of the breeding birds was done by strip, plot, and nest counting methods and territorial maps were determined for each species. In all 96 censuses were conducted on the study areas, and approximately 648 man-hours were spent on the areas. During the study 200 active nests were located of which 125 were periodically examined. Most of the work was confined to the desert floor but a few canyon censuses were made.

No concentrations of nests were apparent in the vicinity of water holes although such species as killdeer and vermilion flycatcher were found only in the vicinity of the small pond at Quitobaquito. These areas were utilized by large numbers of individuals of several species for drinking and bathing purposes.

The white-winged doves were by far the most abundant. Twenty species of birds composed the breeding population of Alamo Canyon.

The four research plots located in the intermountain plains, were divided into two habitat phases: (1) wash and (2) inter-wash areas.

(1) *Wash areas.* A total of 295 transient individuals, representing 18 species were observed on these two areas. Members of the sparrow genus Zonotrichia were the most numerous with the Brewer's sparrow second in abundance during the 78-day migration period (March 3 to May 20).

Breeding populations of the two areas were similar in species concerned, 28 in Area 1 and 29 in Area 2, while the density was considerably higher in the second area (88 to 108 pairs per hundred acres, respectively). The difference in the population density is due to the greater numbers of white-winged and mourning doves nesting in Area 2.

(2) *Inter-wash areas.* Seven species utilized these open areas while migrating. A total of 165 individuals were noted during the 68 day period from February 27 to May 3, with the Brewer's sparrow being the most abundant.

The breeding population of the open desert was considerably lower than in the washes for only 37 pairs per 100 ac. were present in Area 3 while the creosote flat of Area 4 was devoid of nesting birds. A total of 25 species utilized Area 3 for nesting and feeding activities.

Eight nests of the western red-tailed hawk, two of the Harris's hawk and two western horned owl nests were found during the study. All but two were confined to a 75 sq. mi. tract in the south-central part of the Monument. Distances between nests of the red-tailed hawk ranged from 3-6 mi.

April and May appear to be the peak migratory periods through the region with the earlier movements being apparent on the open exposed deserts. As the season advances, the cooler canyons and water holes attract the transient individuals.

The over-all nesting season extended from February 28 to August 15, at least, with the Palmer's thrasher having the most prolonged nesting period (170 days). Active nests of 15 species were found on the four areas, of which five were resident species. About 1.0 breeding birds were sustained per acre in the washes while the open desert supported only .24 individuals per acre.

The Arizona study exhibited a lower bird population per 100 ac. than was the case in studies conducted in the Colorado desert of California. During two seasons the California workers recorded 95 and 124 pairs per 100 ac. while the current study found only 69 pairs for the three areas combined. The data were not closely comparable, however, for the Arizona figure was derived from a compilation of all the study areas (210 ac.) while the California project was a selected plot of 37 ac.

An analysis of the zoogeographic origin of the populations supports, when compared with other desert areas, the tendency to an increase from north to south in the South American element and a decrease in the Old World element is presented by Mayr (1946).

Most available habitats have been utilized by the bird species with the cholla cactus, saguaro, palo verde, ironwood, and mesquite being the favored nest plants. Four types of nests were recorded, namely: (1) conventional open-topped bowl, (2) closed-roofed nests, (3) platform type, and (4) hole nests. In general those species building closed nests were not as selective in choosing nest sites as were those whose open-topped structures needed protection.

Heat and humidity may be more critical factors than drinking water during the hot summer nesting season for the bird species. Water is usually obtainable from the food sources throughout the warmer seasons in the form of the various flowers and fruits of the cactus species, particularly the saguaro.

Territory sizes of the various species were quite uniform for the particular species when the two wash areas were examined but differed widely when contrasted to the open desert. Here all species, with the exception of the cactus wrens maintained territories just slightly larger in open desert than was exhibited, in the wash situations.

The large birds of prey produced the highest nesting success with the red-tailed hawk and western

horned owl having a 100% fledging. One of the Harris's hawk nests fledged only one of the two chicks hatched and marked the only fatality in this group.

A total of 294 eggs were laid of which 235 hatched and 214 fledged from 102 nests on the three areas. Expressed in percentages, 80% of the eggs laid hatched, 72% fledged, 91% of the young hatched fledged, and 70% of the nests were successful. White-winged and mourning doves exhibited the lowest nest success being 42% and 50%, respectively. The phainopepla fledged young from 75% of the nests while the remaining four common nesters (cactus wren, verdin, Palmer's thrasher, and house finch) indicated an 80% success.

Factors responsible for nest losses were primarily predators during the egg and nestling stages and desertions during the egg stage. Coyotes, snakes, ground squirrels, and birds of prey probably account for many of the raided nests. Two cases (verdin and cactus wren) of the fully feathered nestlings dying were recorded but no causes could be determined. At least one fledging (Palmer's thrasher) was known to have perished as a result of being entangled in cholla thorns. Instances of eggs failing to hatch were recorded in four cases, twice in verdin nests and once each in Palmer's thrasher and Sonora gnatcatcher nests.

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THE VERTICAL DISTRIBUTION OF SALT MARSH PHANEROGAMS IN RELATION TO TIDE LEVELS[1]

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INTRODUCTION

The undisturbed salt marsh, once so widely distributed around the margins of San Francisco Bay, is rapidly disappearing before the onslaught of modern industrial demands. Extensive areas are being acquired by commercial salt companies and converted into pans for the recovery of salt from the sea water. Urban expansion on the shores of the bay also takes an increasingly heavy toll of the salt marsh lands with the establishment of sewage disposal units, refuse dumps, airports, residential tracts, and recreational areas.

It seemed of real importance, therefore, to inaugurate in a relatively undisturbed area a study of the vertical distribution of the flowering plants of these marshes in an effort to determine the relationship of their characteristic zonation to their submergence and emergence resulting from the regular rise and fall of the tide.

The area of salt marsh chosen for this investigation lies immediately to the north of the Palo Alto Yacht Harbor and approximately at latitude 37° 27′ N.; longitude 122° 06′ W. It extends from Sand Point to the southern margin of the outfall from the Palo Alto Sewage Disposal Plant, and has an area which is approximately half of a 286-acre tract. This section of the marshlands is owned by the City of Palo Alto.

The help of numerous people has facilitated this work. I wish in particular to acknowledge that of Dr. Ira L. Wiggins, Dr. Richard W. Helm, and my wife, Augusta L. Hinde.

[1] Contribution from the Dudley Herbarium, Stanford University, Stanford, California.

REVIEW OF LITERATURE

The peculiar nature of the salt marsh habitat has long attracted the interest of biologists, but the greater part of this interest has been of a physiological nature, centered upon the mechanisms which enable plants not only to survive but to flourish in a "physiologically dry" habitat.

One of the earliest ecological studies of a salt marsh vegetation on the North American continent was made by W. F. Ganong (1903) at the Bay of Fundy. Both the natural and the diked marshes were considered. The total area of these marshes was not accurately known, but it was estimated to be between 70,000 and 80,000 acres, the greater portion of which was diked and under cultivation. These marshes were found to be "built in a subsiding basin out of inorganic red mud brought in from the sea by the rush of the tides, whose height is the determining factor in their height. Practically no part of their mass has been built from detritus brought down by rivers, which in this region are altogether insignificant in volume; nor has vegetation, either marine or land, helped to any appreciable extent to build them." The tides in the Bay of Fundy may have a range of over 40 ft., with exceptional tides reaching 70 ft.

In the wild or unreclaimed marshland, Ganong found three characteristic formations; the *Spartinetum*, the *Salicornietum*, and the *Staticetum*. The *Spartinetum* extended "as a belt just above and be-

low ordinary high tide mark." Its dominant and only plant was *Spartina stricta glabra* Gray, "the most characteristic and extreme salt-enduring plant of the marshes." It was always found at the margin of the salt water, except in the newest marshes. Its height was stunted to 6 in. on the open sea, and reached a maximum of 3 or 4 ft. in the brackish water of the depressions which were filling with mud. Fertile seeds and seedlings were found to be rare, propagation being primarily by root-stock. By this method the Spartina advanced successfully into the habitat of the *Salicornietum* and destroyed that association, then continued its advance against the *Staticetum*, there in its turn to be overcome.

Ganong described the *Salicornietum* as the "characteristic association of the newly-formed and forming marsh, occurring typically from the lowest high tide marks to the highest marsh, hence overlapping the territory later occupied by the *Spartinetum* from below and the *Staticetum* from above." The *Salicornietum* was found to be composed of two dominant members, *Salicornia herbacea* L. and *Suaeda linearis* (Ell.) Moq. The difference in the location of Spartina and Salicornia is attributed to their relative ability to withstand immersion, the endurance of the Spartina being greater due to its extensive aerenchyma. Ganong considered their salt tolerance to be approximately the same.

The *Staticetum* represented the matured condition, the highest development of the salt marsh vegetation. It was found to occur on the highest parts of all of the wild marshes. Two dominants were recognized in this association, *Limonium carolinianum* (Walt.) Britton, and the fox grass, *Spartina patens* (Ait.) Muhl., the "most abundant and characteristic grass of the high salt marsh. . . ." These, with lesser members of the formation, were found to have moderately xerophytic structure with much-reduced aerenchyma. This was considered to be sufficient explanation for their location on the high marsh where they were rarely immersed.

While Ganong thus sensed the importance of submergence and emergence time in determining the distribution of the salt-marsh flora, he did not determine the actual heights of the tides, nor the hours of submergence and exposure to which the plants were subjected daily throughout a growing season, a year, or any particular period of daylight.

The next work of importance on North American salt marshes was a study of the New Jersey marshes between Manasquin Inlet and Sandy Hook Bay, made by Harshberger (1909). Three types of marsh were distinguished along the northern New Jersey coast; a) that covered at every mean high tide; b) that rarely covered at ordinary tides, but subject to inundation at the slightest change in meteorological conditions; c) that marsh lying above mean high tide and almost completely covered by vegetation. All of these marsh types may be inundated by unusually high tides. The types were thought to evolve from one another, so that almost as soon as the mud flats rose above the surface of the lower tides, plant invasion began. *Spartina stricta maritima* Gray was considered to be the pioneer, and its strong stems held mud and debris around their bases so that the surface was gradually raised until the marsh of the first type became a marsh of the second type. This process of building up continued until the marsh of the third type—the mature salt marsh—was established, and the characteristic zonation of plants had been developed.

Harshberger contributed nothing new to our knowledge of the vertical relation of the plants of the marsh to the height of the tides. He did present a description of the plant associations of an Atlantic coast salt marsh which lay considerably to the southward of the Bay of Fundy, thus showing that the same zonation of plants occurred in New Jersey as in the more northerly region.

The first American study with the specific purpose of relating the height of the tide to the vertical distribution of plants was that which Johnson & York (1915) made at Cold Spring Harbor, Long Island, New York. These investigators set out to determine the exact position of the habitat of each species of salt marsh plant with reference to tidal limits and thereby establish, if possible, the degree to which each species is dependent upon the tide level. A graduated tide stake was placed near the middle of the harbor with the zero point at mean low water. Using this stake as a reefrence, the 5-, 6-, 7-, and 8-foot tidal contours were established on the beach. On the basis of these contours, five plant associations were defined.

The *Spartinetum* of the mid-littoral marsh of Cold Spring Harbor was striking in that it was almost a pure stand of *Spartina glabra* Muhl. It was found to lie exactly between the levels of mean low water and mean high water, which is about 8 ft. above mean low water at Cold Spring Harbor. (Mean low water—M.L.W.—is an average of the two low waters per day over a period of years.) Johnson & York suggested that wherever the vertical distribution of the *Spartinetum* could be accurately determined, it would be found to lie "just about midway between the mean tide-marks" along the whole North Atlantic coast.

The numerous environmental factors which act upon the Spartina to influence its spread both vertically and horizontally were considered to be acting also upon other plants of the marsh. Thus temperature, light, and the nature of the substratum which is more or less the product of the Spartina, could be ruled out as determining factors, leaving the tide levels of primary importance as delimiting factors, augumented or modified by the fresh water entering the marshes, either from springs or streams.

Spartina at its lower limits withstands a submergence of about 8.5 hours at each tide, or 17 hours of daily submergence. At its upper limit, Spartina is subjected to a soil submergence of only 2.5-3 hours per day. This grass then endures a rather wide range of submergence and emergence times. Its spread to higher levels does not seem to be curtailed by increased tidal exposure, but rather by competition with the plants which are able to grow at higher levels.

At the 7-foot level *Salicornia europaea* L. was mixed with *Spartina patens* and the salt grass, *Dis-*

tichlis spicata (L.) Greene, yet at 7.5 ft. Salicornia was almost completely dominant. Elsewhere on the marsh, the glasswort, when it occurred, was found along the margins of the drains and tide pools. A second glasswort, *Salicornia ambigua* Michx., was limited in its distribution from 6.5 to 7.5 ft. above mean low water.

Johnson & York suggested that the lower limits of these glassworts were probably determined by the influence of the tidal change upon aeration, since during high tides the soil is completely saturated with water. A goodly portion of the shoot may also be submerged so that all gaseous exchange through the submerged stomata may be halted. The only available oxygen and carbon dioxide then is held in the aerenchyma. For this reason, Spartina with its well-developed air-storage tissue, was considered to be better able to withstand prolonged submergences than could Salicornia, in which the aerenchyma is practically non-existent. Salicornia must of necessity, then, be limited in its downward spread by the duration of the submergence which it is able to tolerate.

The incoming tide was frequently quite turbid, so that most plants which normally grew below the high water mark were forced to carry on most of their photosynthetic processes during the low tides. Since the high tides often were found to occur near the middle of the day, these plants were deprived of several hours of daylight elsewhere favorable to maximum photosynthesis. While Johnson & York were uncertain as to what part this reduced lighting played in the physiology of the plants, they felt that it might be a delimiting factor so far as the lower limit of distribution was concerned.

Since the work at Cold Spring Harbor, little else has been done in the United States toward relating the vertical distribution of salt marsh plants to tidal changes in water level.

Nichols (1920), in a study of the vegetation of Connecticut, attributed the vertical distribution of seaside plants mainly to differences in tide level. The value of his work lies in his description of the marsh. His efforts to relate the zonation of various plants to tidal changes were of the most general nature only.

Conard's (1935) phytosociological study of plant associations on central Long Island included the salt marsh. He found that salt marshes appeared above the 5-foot level wherever silting occurred. Where the land sloped gently toward the sea, he found the following zone-associations:

1. *Spartinetum glabrae*—5-7-foot tide levels
2. *Salicornietum*—7-7.5-foot tide levels
3. *Distichlidetum*—7-8-foot tide levels
4. *Spartinetum patentis*—7.5-8-foot tide levels
5. *Scirpus americanus*—8-8.5-foot tide levels
6. *Suaedetum*—7.5-8-foot tide levels
7. *Spergularia*—wherever the *Spartinetum patentis* had been killed or where sand and gravel had been placed at the level of the *Spartinetum* to fill tide pools for the control of mosquitoes.

Conard, however, failed to discuss the manner in which he established the tidal levels given here.

The *Spartinetum glabrae* of central Long Island formed a dense meadow of tall coarse grass, constituting the marginal vegetation on muddy shores where the soil is covered with salt water twice a day. The Spartina made its maximum growth and flowering between the 6-7-foot tide level, above which it either stopped abruptly or sent a shorter and weaker vanguard into the next higher association. Below the 6-7-foot tide level it was also poorly developed.

The *Salicornietum* included *Salicornia ambigua* and *S. europaea*. The former was found on the marshes which were broad and gently sloping, while the latter grew upon any denuded area from the 6.5-foot level up to the limits of the high tides.

The salt-grass, *Distichlis spicata*, seemed to take possession of areas denuded by masses of drift, always between the 7-8-foot tide levels.

Other investigators in the United States have also dealt with salt marshes, but none has sought to augment the data pertaining to the effect of tidal movements on vertical distribution, although all have added to the record of the distribution of salt marsh species. Penfound & Hathaway (1938) recognized two salt water communities in the marshlands of southeastern Louisiana. These were the *Spartina alterniflora* Lois. consocies of the saline marshes and the *Spartina-Distichlis-Juncus* associes of the brackish marshes. The slopes of each of their transects, however, was obtained by comparing the water levels in various zones during the periods of high water, when the transects were mostly submerged. By this method, they found that a change in elevation of 3 inches might cause the transition from one community to another.

Reed (1947), in studying the relation of the *Spartinetum glabrae* near Beaufort, North Carolina to edaphic factors, found that at the position normally reached by high tide, there was a transition to the next landward community, either *Distichlidetum* or *Salicornietum*, thus implying that tidal levels are determining factors in the vertical distribution of the *Spartinetum*. The upward spread of this association is also determined by its competition with other angiosperms which are unable to undergo prolonged submergence or a high degree of salinity in the soil solution, and by reduction in the degree of saturation of the soil with salt or brackish water. Poor drainage also seemed to favor the occurrence of the *Spartinetum*.

The investigation of the vertical distribution of phanerogams on the American salt marshes, then, indicates that the rise and fall of the tide, with the resulting submergence and exposure, is the primary factor involved in limiting the vertical range of species. In addition to the direct effect of the tide levels, the vertical range of a species may be influenced by the degree of aeration in the marsh soil, the

salinity of the soil solution, and the character of the substratum itself. It is probable that the distribution of salt marsh phanerogams depends upon the combined effect of these various factors.

In addition, there is evidence of the essential uniformity of structure of the North American salt marshes wherever they occur on this continent. The marginal emergent vegetation consists of a coarse salt grass of the genus *Spartina*. The next shoreward community is a *Salicornietum* composed principally of the annual *Salicornia europaea* on the eastern and Gulf coasts, and of the perennial *Salicornia ambigua* on the Pacific coast. The salt-grass may appear in pure stands on the marsh or, as is more general, may have a scattered distribution. It is found on the marshes of the eastern seaboard, the Gulf coast, and the Pacific coast. Other plants may occur in the vast marsh areas of our coasts, but they are invariably of lesser importance and more subject to regional variation.

Salt marshes have long occupied the attention of European investigators too, but for many years their chief interest was in physiological mechanisms. In England during the past 40 years however, great interest has developed in the factors affecting the vertical distribution of plants on the marshes. Marsh (1915) described the societies of the marshes of Holm-next-the-sea, Norfolk, in the order of their vertical occurrence. Yapp, Johns & Jones (1917) simplified the vegetational description of the salt marshes by identifying five main zones in the marshes of the Dovey Estuary. These five zones were found to have a combined vertical range of less than 4.5 ft. Yapp *et al.* stressed the importance of the frequency and duration of tidal submergence in determining vertical distribution on the salt marsh, but they were more interested in "phytological problems" on the marsh—the effect of salt marsh plants in modifying and controlling ordinary geologic processes—and so did not pursue the effects of tidal change farther.

In the past two decades, however, V. J. Chapman has devoted much time to the study of salt marsh ecology and over a number of years has given much attention to the factors affecting vertical distribution on the marshes. His initial studies (1934) were concerned with succession on the marshes of Scolt Head Island, Norfolk, and the factors he considered to be fundamental in influencing that succession—tidal submergence and emergence. In investigating this "compound factor," Chapman obtained a complete series of tide curves for July-October, 1933, and used them to calculate the hours of submergence and emergence for the ecologically important levels of the marsh—levels which represented the upper and lower limits of the different plant communities and species. The levels were obtained through the use of a levelling survey. All of his tidal data for Scolt Head Island is based on an arbitrary datum, Island Zero Level, which is equivalent to 7 ft. Ordnance Datum. The marshes fall into two distinct zones. The upper marshes lay above 1.10 I.Z.L., and the lower marshes lay below that level. It was found that nearly all species and communities occurred either above or below 1.3 I.Z.L. and rarely included this level in their range. Hours of submergence were found likely to be of great importance in controlling distribution at the upper levels, while the hours of emergence seemed to be more important in the distributional control at lower levels. None of the higher plant associations or species investigated had a lower limit below mean sea level.

After further study, Chapman (1938) concluded that there are 10 major environmental factors operating on a salt marsh. These factors are not independent in their action, hence all must be considered. They are:

1. Tides	6. Rainfall
2. Salinity	7. Soil
3. Drainage	8. Evaporation
4. Aeration	9. Temperature
5. Water Table	10. Biota

Of these ten factors, Chapman considered the tidal influence to be the major one.

Twelve species of phanerogams studied were found to occur on either the upper marsh or the lower marsh exclusively, while 6 were found on both upper and lower. Of the algae studied, 27 species occur almost entirely on either the upper or lower marshes, while 9 were found on both. The upper marshes have characteristically a long tidal exposure in summer when drying can be severe, thus algae occurring there were those species particularly suited to tolerate desiccation. Only two phanerogams were found to extend below—1.00 ft. I.Z.L., at which point submergence during the daylight hours becomes an important factor.

In conjunction with his study of tidal factors, Chapman (1938, 1939) also went deeply into the problems of water table, soil aeration, drainage, and soil salinity.

During 1935-36, Chapman made a study of the Romney Salt Marsh near Boston, where he found that in spite of the wide differences between the American marshes and those of Norfolk, certain similarities were marked. Tide levels on the Romney marsh were read from a graduated stake in one of the creeks of the marsh, then correlated with the tidal movements as obtained from the tide gauge in Boston Harbor. He found that Romney Marsh could not readily be divided into an upper and a lower marsh as could the salt marshes of Norfolk. At about 9.4 ft. above mean low water, however, he found a marked change in the maximum period of tidal exposure. Below that level, the exposure period was 8 days, while immediately above it, the exposure was 16 days per month. The long periods of exposure above 9.4 ft. occurred during the late winter, so that the plants were exposed to extreme cold rather than to the summer desiccation characteristic of the Scolt marshes.

On both the Romney marsh and at Cold Spring Harbor, the only phanerogam with a lower limit be-

low mean sea level was *Spartina alterniflora* (2.81 ft. on Romney marsh and 1.5 ft. at Cold Spring Harbor). None of the phanerogams of Romney marsh, except Spartina, Zostera, and Ruppia extended below 7.81 ft. where they would experience an average daily submergence during daylight of 4 hours. The maximum submergence in daylight that any species could bear was about 14 hours per day.

Chapman felt that it was characteristic of American species that "the farther south they spread on the continent the more tolerant they are of submergence (i.e. the lower they go in relation to the tidal plane)." This suggested to him that the tidal phenomena are not completely responsible for determining vertical distribution, but that temperature may also be effective.

As a result of Chapman's work, and those before him, the structure of the salt marshes of the East coast of England may readily be contrasted with the marshes of North America. Whereas the genus *Spartina* is always found as the emergent plant on American salt marshes, the genus *Salicornia* appears to be the emergent on British marshes of the East coast. As soon as the silt flats upon which algae grow have been raised out of the waters for a portion of the day, Salicornia colonizes the mud and a *Salicornietum* is established (Chapman 1934). The next shoreward association is the *Asteretum* which gives way on its landward side to a General Salt Marsh, on which a number of plants such as *Spergularia media* (L.) C. Presl. and *Triglochin maritima* L. may be co-dominant. The General Salt Marsh merges at its upper limits into a so-called "sea-meadow"—a *Glycerieto-Obionetum*.

The highest marsh community is the *Juncetum* which is dominated by *Juncus maritimus* Lam. (Chapman 1934)

Chapman (1934) stated that on Scolt Head Island, Norfolk, *Spartina stricta* Roth was observed in 1925 as two or three small patches in the *Asteretum*. By 1933, one of these patches had become quite extensive and other groups of the plant were to be found so that it appeared to be spreading. It was conceivable to Chapman that the result might be a resemblance to the marshes of the East coast of North America, where *Spartina* species play such an important role on the lower marsh.

Just such an event has been occurring along the southern coast of England during the past hundred years or so. *Spartina stricta* is indigenous to that coast, but formerly occurred only here and there. About 1836, however, *Spartina alterniflora* was introduced, probably by shipping (Arber 1934). By 1870 a new Spartina, *Spartina townsendi* Groves, was discovered. This new cord-grass is now recognized as a hybrid from a crossing of *Spartina stricta* and *Spartina alterniflora*. It has spread east and west with true hybrid vigour along the southern coast of England since its first appearance, until vast areas of soft mud flats are clothed with cord-grass. In 1906, it was first noticed on the Normandy coast, and within 15 years it had occupied over 20,000 acres in the Baie des Veys—acres which formerly were barren flats of soft tidal mud.

Spartina townsendi colonizes the mud from a "little below high water at spring tides to a line about a metre below this level; six hour's consecutive immersion per tide seems to be the most that it can endure. According to whether the slope is rapid or gradual, the belt occupied may vary from some metres to some kilometres in breadth" (Arber 1934).

Townsend's grass is of great economic importance in southern England and Europe because of its land-building abilities. Its rapid spread will almost certainly change the face of the salt marshes of England and Europe as they are known today.

DESCRIPTION OF AREA

That portion of the Palo Alto Salt Marsh with which this study is concerned has a maximum elevation of 10.4 ft. above mean lower low water (Cf. Tidal Movements). Its outer margin is bound by a levee constructed in 1936, which has since that time partially protected the region from tidal floodings.

The marsh is drained by an intricate network of creeks of varying size, the smaller converging to form larger ones, which in turn anastomose to form several major creeks or drains which empty into the bay through breeches in the dike (Fig. 1). The small shallow creeks, often no more than depressions in the surface of the soil, are completely filled with *Salicornia ambigua*. The larger streams, however, form deep and tortuous gullies, some as much as 4 ft. deep and several feet wide, winding through the marsh. Both sides of these drains may be perpendicular, or they may vary, that side which receives the force of the tidal current being undercut and cliff-like, while the opposite bank is shelved and falls away more gently toward the bed. The undercut bank usually supports a luxurious growth of glasswort which hangs over the edge in a matted tangle, giving the impression of secure footing to the uninitiated and forming a well-protected nesting place for rails and other marsh birds. The luxuriance of the Salicornia along these creek banks is probably a result of the aeration of the roots afforded by the numerous crab burrows with which the banks are perforated, and to the comparatively rapid drainage of the undercut margins.

The shelved banks of the creeks usually support a stand of cord-grass which may invade the muddy bottom of the drain if its depth is no greater than 6.4 ft. above mean lower low water (Figs. 2A & 2B). The matted rhizomes and roots of Spartina form an effective barricade against the erosive effects of the tidal current as it flows up the creeks. Mussels, snails, and small crabs live among the stalks of cord-grass. The very deep creeks have no seed plants growing on their soft mud bottoms, although algae may be present in those which contain relatively quiet water (Plate I, B).

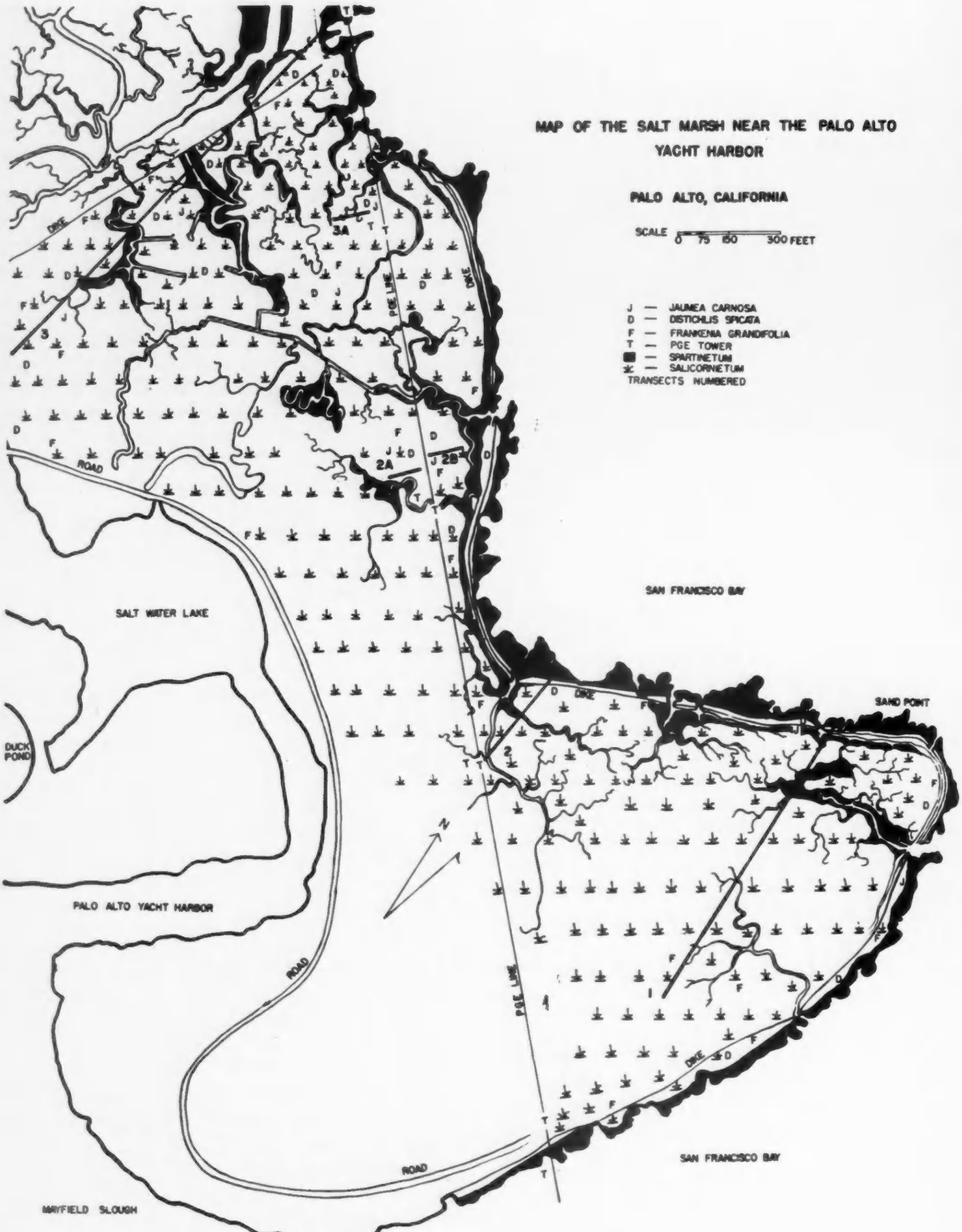

FIG. 1. Map of the area showing intricate network of creeks draining the marsh and distribution of dominant flowering plants.

FIG. 2A. One of the larger drains. *Spartina leiantha* growing on the left shelved bank. *Salicornia ambigua* on the right undercut bank and overhanging the drain.

FIG. 2B. A broad and rather shallow drain. *Spartina leiantha* on left bank. Note that it fills the shallower end. *Salicornia ambigua* overhanging right bank; algae on muddy bottom.

It is mainly by means of these streams that the tides have access to the marshes, either flooding the ground or raising the water table to such an extent that water stands on the surface. Inundation regularly occurs during the highest tides, as is indicated by the great amount of tidal debris—dried herbaceous stems, logs, old pilings, bottles, oil cans—left high on the marsh.

TIDAL MOVEMENTS

All tidal data for the area of salt marsh studied are referred to the datum of mean lower low water, the average height of the lower of the two low waters for each day over a period of 18.2 years. Elevations of the tide planes referred to this datum at the Palo Alto Yacht Harbor, then, are as follows:

Highest tide (estimated)	11.0 ft.
Mean higher high water	8.4 ft.
Mean high water	7.8 ft.
Half tide level	4.5 ft.
Mean low water (M.L.W.)	1.2 ft.
Mean lower low water (M.L.L.W.)	0.0 ft.
Lowest tide (estimated)	−2.5 ft.

Half tide, a plane midway between high water and mean low water, differs from mean sea level, the average height of the surface of the sea for all stages of the tide, by only a few hundredths of a foot, and for all practical purposes the two may be considered to be the same.

The salinity of the water at Dumbarton Bridge during the month of July was found by Miller *et al.* (1928) to decrease on the flood tide and increase on the ebb, with the highest salinities at the approximate time of slack low water. Thus the salinity of the relatively shallow portion of the bay south of Dumbarton Bridge is increased by 1 to 2 p.p.t. by evaporation in the summer time.

SOIL

The soil of the marsh is Galveston Clay (Cooper 1926) and represents a deposition of the finest particles borne by the streams draining the Santa Cruz Mountains. It is a stiff clay which is quite treacherously mucky when wet. When dried, however, it becomes very hard, shrinks extensively, and in doing so cracks over its entire surface into a striking polygonal pattern. The soil is poorly drained and poorly aerated, anaerobic conditions prevailing just beneath its surface, as is indicated by its blue-black color and a strong odor of hydrogen sulfide given off whenever the clay is disturbed. The water table lies either at the surface or only slightly below the surface.

In the *Spartinetum* there is little peat, but the soil of the *Salicornietum* and of those areas showing a mixed vegetation such as *Distichlis spicata*, *Jaumea carnosa* (Leiss.) Gray, and *Frankenia grandifolia* C. & S. contains considerably more peaty material.

VEGETATION

Cooper (1926) described the salt marshes of the San Francisco Bay as the marginal community of the native vegetation supported by the alluvial fans of the creeks flowing into the bay. He found this community to retain much of its original character. In the years that have passed since Cooper's study however, the changes mentioned in the section on the secular history of the area have been made, and to a greater or lesser degree have influenced its vegetation. In spite of these changes, the dominant plants remain the same.

The pioneer plant on the lowest reaches of the marsh is *Spartina leiantha* Benth. It advances onto the soft mud of the tidal flats where it is subjected to inundation by every tide, grows luxuriantly along the sides and bottoms of all but the deepest drains, and forms dense stands with canes up to 40 in. in height in low-lying areas which are subject to frequent inundation by the tide (Figs. 2 & 6). Flowering occurs from late July or early August through October. Its major means of propagation is by underground rhizomes which form a dense mat in the mud of the *Spartinetum*. No seedlings were found.

Salicornia ambigua is the dominant plant of the salt marsh from the middle elevations upward. It is the most widely distributed of all of the plants of the marsh, and over extensive areas forms a dense pure stand. Its most luxurious growth, however, is attained along the margins of the drains and in other regions wherein the soil is comparatively well-drained and well-aerated due to the presence of crab burrows or channels left by decaying root stalks. *S. ambigua* is markedly succulent during the spring and summer, but as the year advances the tips become bright red in color and the succulence of the stems is gradually lost, being replaced by dry woody tissue. Throughout the rainy season, the tips remain fleshy, and very early in the year succulent growth begins again.

The glasswort is parasitized by *Cuscuta salina* Engelm. which grows in masses of considerable size on the upper tips of the branches of Salicornia, forming bright orange patches across the *Salicornietum* during the greater part of the summer. *S. ambigua* is a perennial which propagates itself by seeding. In the early spring—February and March—many seedlings may be seen, particularly on the areas which are otherwise free of vegetation as a result of reclamation activities. Salicornia therefore might well be considered to be the landward pioneer, moving into areas of reclaimed land which lie within the limits of its range.

Distichlis spicata occurs in pure stands in some areas on the marsh. It is frequently found growing with *Jaumea carnosa*. Both are generally restricted to areas which are not subject to frequent inundations by the tide, such as the tops of levees, but both may grow with considerable luxuriance in areas subject to some tidal flooding.

Frankenia grandifolia is quite widely distributed on the marsh. It reaches its best development, however, along the margins of the dikes and in other localities not subject to frequent inundation.

Triglochin concinna Davey is found in the same general areas as Frankenia, but with far less frequency, only small and isolated patches being found on that portion of the marsh studied.

Limonium californicum (Boiss.) Small occurs in this section of the marsh, but with considerably less abundance than it was found by Cooper in 1926, it would seem, for he described it among other plants as occurring "throughout in more or less abundance." Some of the other plants which he listed in the same category were *Plantago maritima* L. and *Triglochin maritima*, but they were not recorded during this study. *Grindelia cuniefolia* Nutt. is still to be found scattered about the higher elevations of the marsh, but its place in the community is apparently a minor one.

Plants which have come into the area, possibly as a result of its partial reclamation following the building of levees, include *Chenopodium ambrosioides* L., which is found most abundantly along the roads and in areas which have been raised above the level of all but the very highest tides. Yet, in several places, it is advancing into the marsh, even onto soil which is wetted by each high water. *Atriplex semibaccata* R. Br., *Cotula coronopifolia* L., and *Spergularia marina* (L.) Griseb., have also invaded the reclaimed margins of the marshy area and the tops of the dikes, but seem to be of no importance upon the marsh proper.

Along the outer margin of the marsh a bank several feet in height, the product of the undercutting action of the waves and currents at high tide, has been formed. The edges of this bank are gradually being moved landward as undercut chunks fall because of their own weight onto the mud below, carrying with them a mat of cord-grass which does not take root in the new locality but invariably dies. This constant extension of the cliff-like walls to the landward is resulting in the breeching of the dikes in numerous places, as has already been described.

HISTORY OF AREA

GEOLOGICAL HISTORY

The salt marshes on the west side of San Francisco Bay are built upon the extensive alluvial deposits of the streams draining the eastern slopes of the Santa Cruz Mountains. The largest of these alluvial fans are from San Francisquito Creek, which has a basin of 37 sq. mi., and Stevens Creek, with a basin of 28 sq. mi. (Branner 1909). The salt marshes around Palo Alto Yacht Harbor are located entirely on the alluvial fan of San Francisquito Creek.

During the Tertiary, there were apparently movements along the San Andreas fault zone which resulted in the uplifting of an extensive area west of the fault. A barrier, either complete or partial, was thus formed across the streams draining the San Joaquin and Sacramento Valleys. As a result, a great inland lake of fresh water developed, extending down the Santa Clara Valley, and perhaps even into the San Benito Valley.

The uplifting was followed in the Quaternary by a general subsidence, in places to a position as much as 2,000 ft. below the present level. The outlets from the inland lake were submerged and the sea moved in, converting the fresh water lake into an arm of the sea, the present Bay of San Francisco.

Late in the Quaternary, the coastal region underwent another uplifting, this time to positions higher

than the present elevation. Streams draining the mountains thus formed began carrying their silt down into the Santa Clara Valley and on into the bay, so that both during and since this last coastal upheaval, the bay has been in a gradual process of silting up, while the alluvial fans built by the streams have been covering salt and brackish water deposits around the edge of the valley, and have encroached upon salt water deposits along the bay shore, often to a depth of 200 ft. (Branner 1909). Thus San Francisco Bay has been gradually filled with silt around its margin, so that at present that portion of the bay south of Dumbarton Bridge consists of extensive mud flats at low tide. These mud flats are traversed by a main channel which does not exceed 50 ft. in depth at its deepest point at mean lower low water, and by a number of lesser channels leading from the larger creeks draining the marshes. These lesser channels vary at their deepest point from 13 to 21 ft. at mean lower low water, and may reach a depth of only 1 ft. at that time in their shallowest places.

SECULAR HISTORY

During the early part of the past century, when the southern reaches of San Francisco Bay were the scene of extensive sailing activities, a landing was built at the mouth of San Francisquito Creek. But it was used very little, probably because of the shallow water. Another landing was built on the banks of Mayfield Slough in 1873 to facilitate the shipping of produce to San Francisco. With the construction of the San Francisco-San Jose Railroad, however, the need for sails dwindled and for nearly 50 years, the salt marshes near Palo Alto were disturbed only by hunters and fishermen.

In 1921, the City of Palo Alto purchased 40 acres of marshland bordering on Mayfield Slough. In 1926, the city bought another block of marshland and immediately began a program of reclamation which included dike building and dredging to convert the slough into a yacht harbor. The dredged mud was placed back of the dikes and given an opportunity to leach, while at the same time increasing the elevation of the marshy land.

By 1929, the excavation of the Palo Alto Yacht Harbor was completed. Contiguous land lying to the North and West of the yacht basin was filled with 270,000 cu. yd. of mud from the slough, thus raising the average level to 4 ft. above that of the surrounding unreclaimed marshland.

In 1936, levees were raised for some distance around the shoreline of the bay, and 5 years later they were increased in height by about 3 ft., to an approximate height of 8 ft. above the level of the tidal flats.

The construction of the dike enclosed a basin of 240 acres in which the silt from San Francisquito Creek is deposited. The plan is completely to reclaim this land, now largely mud flats covered by sea water except at low tide, after a period of from 25 to 30 years.

In the building of the dike, the mouths of the larger creeks draining the impounded marshland were apparently left open to the sea, thus permitting the tide to enter and cover periodically the areas within its reach, so that the salt marsh has been able to maintain itself at least to a major extent.

In recent years, the dike has fallen into disrepair. Since 1949, large sections have been eroded away by the action of the waves, and the sea is gradually gaining a freer access to the impounded marshes. At the time of this writing, however, work has begun again on the marsh and portions of the area under investigation are being changed considerably by the construction of new channels and levees. To what extent this will change the character of the marsh remains to be seen.

METHODS

To relate the vertical distribution of the plants on the salt marsh to the influence of the tides, it was necessary to determine the extent of each association and the elevations of each zone above mean lower low water. Pure stands characterized each zone and the line transect was used as a means of recording the vertical distribution.

Six line transects were run, each beginning at the upper margin of the marsh and extending toward the bay across the zones of vegetation. A measuring tape was laid out along the line of the transect, and a stake was driven at each 10-foot mark. A permanent transect was thus established which could be revisited from time to time for various purposes. A record was made of the plant occurring at each one foot interval over the full length of each transect.

Transect No. 1 ran across the marsh for 956 ft., ending at the tidal bank on the outer margin of the marsh. It was destroyed by dredging operations in the Palo Alto Yacht Harbor before it could be used.

The second transect was established approximately 900 ft. to the northwest. It extended across the marsh for 550 ft. to end in the very soft mud of the tidal flats at a point where the cord-grass is advancing bayward across the mud.

The next three transects—2A, 2B, and 3A—were each 100 ft. in length and were laid out so as to bisect the zones of vegetation, including areas of transition in which a mixture of plants occurred.

The fifth and final transect—Transect No. 3—was the longest and passed through a much more diversified area than did any of the others. It was 1450 ft. long.

Plants along the transects were recorded and the area was surveyed with a transit and rod to determine the exact elevation of each 10-foot marker on each of the transects. The levels obtained from the survey were related to U. S. Coast and Geodetic Survey Tidal Bench Mark, No. 1, 1931, at an elevation of 10.71 ft. above mean lower low water.

By using the elevations thus obtained in conjunction with a continuous hourly record of the tidal rise and fall, taken mechanically for one year at the

Dumbarton Bridge by the U. S. Coast and Geodetic Survey in 1936-37, it was possible to determine the average submergence and emergence times per calendar month per tenth of a foot elevation, as well as other data pertinent to the relationship between plant and tide level.

RESULTS AND DISCUSSION

Chapman (1934), in his study of the marshes of Scolt Head Island, Norfolk, classified the marshes phytosociologically as being of two kinds; a) those with a wide frontage open to the sea, and b) those which were closed, where the tide has access to the marsh through a narrow channel. Closed marshes induce more rapid silting, because the tidal waters rush in through narrow channels, then quickly slow down, depositing their silt as they spread over the surface of the marsh.

The presence of well-developed creeks indicates that the Palo Alto marshes were closed marshes in their natural state. Most certainly they became closed marshes in 1936 when the levee was built along their outer margin, forcing the tide to enter through the creeks whose mouths remained open to the bay through the dike. At present, however, it is probable that they are in the process of becoming open marshes, at least in sections where tidal erosion has been so extensive that wide breaches have been made in the dike, enabling the rising tide to flow directly onto the marsh at these points. Erosion is continuing at a rapid rate and will soon open large sections of the marsh to direct flooding by the tides unless the dikes are repaired.

THE TRANSECTS

The survey of the area of salt marsh near the Palo Alto Yacht Harbor showed that there is a gradual rise in elevation from the outer margin of the marsh toward the land (Figs. 3 & 4), and that the entire area lies below the 10.3-foot level. The dike which was contructed along the outer margin of the marsh to the mouth of San Francisquito Creek lies across the bayward ends of Transects No. 1 and 2.

Transect No. 1 was located about 200 ft. west of the dike. The *Salicornietum* at that point was broad, with *Frankenia grandifolia* occurring occasionally and orange patches of *Cuscuta salina* prominent over the higher elevations during the spring and summer. Toward the bay, the cord-grass became more abundant until the *Spartinetum* proper was established. The *Spartinetum* and *Salicornietum* alternated with one another from this point on to the dike. In general, the *Spartinetum* was marginal along the creeks with the *Salicornietum* occupying the areas between.

The portion of the marsh lying immediately to the landward of the levee supported a dense growth of Spartina. Along the sides and top of the dike, both *Distichlis spicata* and *Jaumea carnosa* grew luxuriantly. Beyond this, a pure stand of Spartina extended toward the bay from the dike, then ended abruptly at the edge of a tidal bank which stood 51

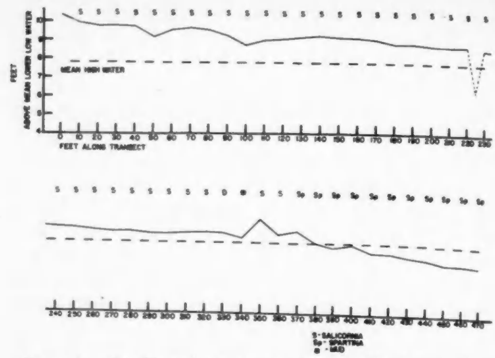

FIG. 3. Profile of transect no. 2. Numbers along ordinate represent feet elevation above M.L.L.W.; those along abcissa represent, in feet, position of stations along length of transect.

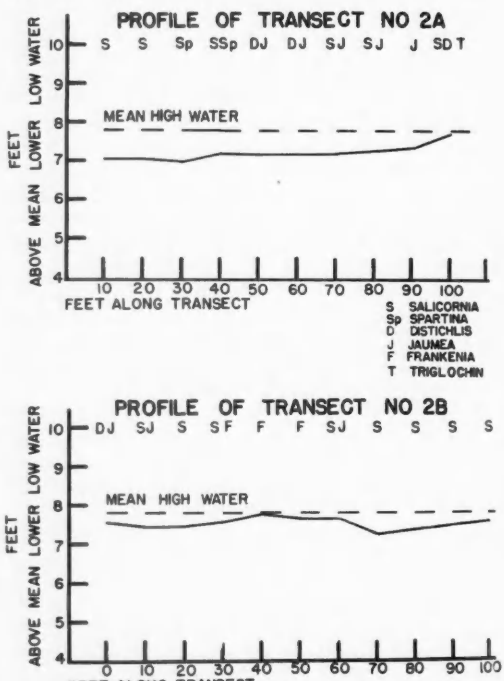

FIG. 4. Profile of transects 2A and 2B. Graphs are essentially profiles of the sections of marsh which transects cross.

in. above the tidal mud flats. The bank was being undermined constantly by the action of waves during high tides, so that large chunks of the *Spartinetum* would fall onto the mud below, where the Spartina eventually died.

On the bayward side of the dike crossing Transect No. 2, the land lies generally below the level of mean high water and supports a pure stand of *Spartina leiantha*, whereas to the landward, the marsh lies uniformly above the level of mean high water and supports an extensive and nearly pure stand of

Salicornia ambigua. Along the top and sides of the levee, *Distichlis spicata, Frankenia grandifolia,* and *Jaumea carnosa* may be found.

The landward end of Transect No. 3 lies 9.4 ft. above mean lower low water. This transect crosses a section of the marsh which is not protected by a levee along its outer margin. It has, however been subject to rather extensive human operations. A dike, built along San Francisquito Creek, is crossed by Transect No. 3 and is also broken through in numerous places by large creeks through which the tides have access to this part of the marsh. Tributaries from these creeks wind through the area which lies generally at the level of mean high water. The vegetation is more varied than the region of Transect No. 2, where the elveation on the landward side of the dike lies above the level of mean high tide. In addition to extensive areas of glasswort and cord-grass, *Distichlis spicata* occurs widely, occasionally in pure stands, and often mixed with *Frankenia grandifolia, Jaumea carnosa,* rarely with stands of *Triglochin concinna,* and occasionally with plants of *Limonium californicum.* Such an area might be considered comparable to the General Salt Marsh of Chapman (1934), in which there are a number of co-dominants.

Throughout the length of this transect, *Salicornia ambigua* is generally found above the level of mean high water. Where the glasswort does descend below that level, it is either mixed with the cord-grass or the individual plants are separated by bare muddy spaces and matted with algae. The glasswort never reaches its optimal development under these conditions.

Transects Nos. 2A, 2B, and 3A were established to bisect transition zones between two associations. Both transects 2A and 2B lie below the level of mean high water, and along both Salicornia is found. There are however, numerous plants which are either dead or matted with algae on the mud, and none of them reach the 18 or 20 in. in height characteristic of more vigorous plants.

The major portion of each transect passes through a mixed vegetation consisting of *Distichlis spicata, Jaumea carnosa,* and *Frankenia grandifolia* with an occasional plant of Salicornia or *Triglochin concinna.*

Transect 3A lies entirely above the level of mean high tide. It passes through a transit'on between the *Spartinetum* and an area in which *Distichlis spicata* and *Jaumea carnosa* are co-dominants. The glasswort occurs occasionally along the first part of the transect in the tension zone.

An analysis of the transects then establishes the vertical distribution of the salt marsh phanerogams as follows:

Salicornia ambigua has a vertical range of 3.95 ft., its highest recorded occurrence being at 10.3 ft. above M.L.L.W. This is a considerably greater vertical range than the 0.5-foot range of the same species at Cold Spring Harbor (Johnson & York 1915). Johnson & York however, suggested that the glasswort might be capable of a much greater vertical range in a locality more favorable to its growth. At the Palo Alto Yacht Harbor, Salicornia extends somewhat higher onto the marsh than the recorded 10.3-foot elevation, where it becomes mixed with and finally gives way to the plants of the higher levels, such as *Chenopodium ambrosioides* and *Atriplex semibaccata,* most of which seem to have followed the roads into the marshes. Neither Scirpus nor Juncus was found at the upper margins of the marsh, as was described by investigators for marshes on the eastern coast of the United States (Johnson & York 1915; Conard 1935) and on the East coast of England (Yapp *et al.* 1917; Chapman 1934). Johnson & York record *Scirpus americanus* Pers. at 8 ft. M.L.W. while Chapman (1938) records a *Juncetum* between 2.77-3.49 ft. Island Zero Level (equivalent to 9.77-10.49 ft. Ordinance Datum) on the marshes of Norfolk. If, as Chapman (1934) believes, the *Juncetum* represents the final successional phase of the marsh, the marshes around Palo Alto Yacht Harbor have not yet reached their final phase of development. It also seems likely that, because of changes resulting from reclamation, they may be prevented from doing so.

Spartina leiantha extends from 8.4 ft. above M.L.L.W. to 5.4 ft. above M.L.L.W. on the Palo Alto marshes, thus having a vertical range of 3.0 ft. This range is considerably less than the 5-foot range of the related *Spartina glabra,* the dominant seed plant of the marshes at Cold Spring Harbor, which ranges from 1.5 to 6.5 ft. above M.L.W. (Johnson & York 1915), but it closely approximates the 2.6-foot vertical range of *Spartina alterniflora* var. *pilosa* (8.1 to 10.7 ft. above M.L.W.) on the Massachusetts marsh (Chapman 1940). *Spartina glabra* has a vertical range of 4.5 ft. (7.8 to 12.3 ft. above M.L.W.) on the Romney marsh. The highest occurrence of *Spartina leiantha* on the Palo Alto marsh is 0.3-foot higher with relation to the tidal plane than is the minimum occurrence of *Spartina alterniflora* var. *pilosa* on Romney marsh. The cord-grass *Spartina alterniflora* however, descends to 2.81 ft. above M.L.W. on the Romney marsh (Chapman 1940), a tremendous vertical range exceeded only by the descent of *Spartina glabra* to 1.5 ft. above M.L.W. at Cold Spring Harbor.

	Salicornia ambigua	*Spartina leiantha*	*Distichlis spicata*	*Frankenia grandifolia*	*Jaumea carnosa*
highest occurrence	10.35 ft.	8.4 ft.	10.2 ft.	10.35 ft.	8.5 ft.
lowest occurrence	6.4 ft.	5.4 ft.	7.15 ft.	7.55 ft.	7.15 ft.

As has been mentioned, Chapman suggested that the farther south American species spread on the continent, the lower their occurrence with reference to the tidal plane. The distribution of Spartina on the salt marshes of San Francisco Bay however, does not seem to conform to Chapman's generalization, perhaps because of the cooling influence of the California current which sweeps down the coast from the north to Point Conception. The marshes along the eastern coast south of Cape Cod are, in contrast, subjected to the warming influences of the Gulf Stream. *Spartina glabra* at Cold Spring Harbor descends slightly over one foot lower than *Spartina alterniflora* on the Romney marsh, but at Palo Alto, which is considerably farther south than Long Island, *Spartina leiantha* falls some 3.8 ft. short of equalling the lowest occurrence of *Spartina alterniflora* at Romney. The maximum submergence time of the lower margin of the *Spartinetum* of the Palo Alto marshes may amount to 21 consecutive hours when the low water separating two high waters is not low enough to expose the 5.4-foot level above M.L.L.W. On the Romney marsh *Spartina alterniflora* endures an average submergence per day of 16.25 hours at 2.81 ft. above M.L.W., while *S. glabra* on the marsh at Cold Spring Harbor endures an average submergence of 8.5 hours at each tide, or 17 hours of submergence daily. Thus it seems that the submergence time to which the Spartinas are subjected is a controlling factor in their lower occurrence with reference to the tidal plane.

Distichlis spicata on the Palo Alto marsh has a vertical range of 3.1 ft. extending from 10.2 ft. down to 7.1 ft. above M.L.L.W. On the Romney marsh it was found to have a range of 2.5 ft. (11.2 to 8.98 ft. above M.L.W.), while at Cold Spring Harbor, its vertical range was 1.7 ft. (6.5 to 8.2 ft. above M.L.W.) On both the Palo Alto and the Cold Spring Harbor marshes, its minimum level of occurrence is lower with reference to the tidal plane than it is on the Romney marsh.

Jaumea carnosa ranges from 1.7 to 8.5 ft. above M.L.L.W. on the Palo Alto marsh, while *Frankenia grandifolia* ranges from 7.5 to 10 ft. or higher. Neither of these plants has been recorded from either the English marshes or from those of the eastern coast of the United States.

Relation of Tide to Vertical Distribution of Vegetation

Chapman (1934, 1938) found that the Norfolk marshes were divisible into an upper and a lower marsh, each of which exists under different conditions of submergence and emergence. The upper marsh had its periods of maximum submergence at the spring and autumn equinoxes, with a long period of summer emergence during which desiccation could be severe, while the lower marsh had a long period of submergence in the summer. On the Norfolk marshes, 1.10 ft. Island Zero Level (8.10 ft. Ordnance Datum) was considered to be the elevation at which the marshes were divisible.

Chapman could not easily divide the Romney marsh near Boston into an upper and a lower marsh. He did find, however, that at 9.4 ft. above M.L.W. there was a striking change in the maximum period of emergence. The marsh lying immediately below this level had a maximum tidal emergence of 8 days per year, while immediately above this level there was a maximum emergence of 16 days per year. This he tentatively considered to be a basis for dividing the marsh. Chapman's analysis of the tidal phenomena of Cold Spring Harbor, as presented by Johnson & York (1915), showed that those marshes could be divided at about 7.76 ft. above mean low water. Immediately above this level, the maximum period of emergence was 16 days, while immediately below it the maximum period of emergence was 8 days.

An analysis of the tidal data for various levels on the Palo Alto salt marsh (Table I) shows that this marsh cannot be divided into an upper and a lower portion. All levels except 10.3 ft. and 9.4 ft. are submerged at every high tide, and all have their periods of maximum submergence in the late spring, midsummer, and autumn. The months during which the maximum exposure to air occurs are in all cases, except at 10.3 ft. above M.L.L.W., the winter months of December and January, when the rains are unusually heavy. Thus rather than being subjected to excessive desiccation, the higher levels of the Palo Alto marsh are exposed to an abundance of fresh water in the form of rain, which might be expected to influence markedly the salinity of the soil and the percentage of soil moisture. Even the duration of emergence during the daylight hours shows such a gradual decline that there is no point at which a division into upper and lower marshes is definite.

Figure 5, however, indicates that above 7.4 ft. above M.L.L.W. the maximum period of emergence of the vegetation from the tide during the daylight hours occurs in June, while below the 7.4-foot level the maximum period of emergence during the daylight hours is in April. At the 7.4-foot level, the number of hours emergence per month shows little variation from April through July, after which there is a sharp increase in submergence. This latter level, then, might be considered as a dividing point in the marsh, but only insofar as daylight emergence and submergence are concerned. Certainly there is no indication that the distribution of Salicornia and Spartina is affected, for Spartina ranges a foot above while Salicornia extends a foot below the 7.4-foot level.

It is possible that the uniform gradation of this marsh is a result of its construction upon an alluvial fan, and is therefore a characteristic peculiar to the San Francisco Bay region. Further studies of the marshes of the Pacific coast are necessary before a wholly adequate comparison can be made with the marshes of the east coast of the United States and England, for which the data are more complete.

TABLE 1. Analysis of tidal data for various levels on the Palo Alto Salt Marsh.

Level in Feet Above M.L.L.W.	Number of Submergences per Year (Total 708)	Total Submergence per Year Hours	Average Submergence per Calendar Month Hours	Total Emergence per Year Hours	Average Emergence per Calendar Month Hours	Total Emergence in Daylight per Year Hours	Average Emergence in Daylight per Month Hours	Months of Most Frequent Submergence	Months of Most Frequent Emergence	Ratio *Emergence* / Submergence
10.3 Highest *Salicornia*	552	1753	146.08	7107	592.25	4001	333.4	May, July, Aug., Oct.	Dec., Jan., March	4.05
9.4	666	2855	237.91	5905	492.08	....	......	May, July Aug., Oct.	Dec., Jan.	2.07
8.4 highest *Spartina*	708	3901	325.08	4857	404.75	2807	233.9	May, July Aug., Oct.	Dec., Jan.	1.25
7.4	708	4922	410.16	3838	319.83	2147	178.9	July, Aug., Sept., Oct.	Dec., Jan.	0.78
6.4 lowest *Salicornia*	708	6026	502.16	2734	227.83	1477	123.08	May, July Aug.	Dec., Jan.	0.45
5.4 lowest *Spartina*	708	7039	586.58	1721	143.41	988	82.33	Mar., July Aug.	Dec., Jan.	0.24
5.0	708	7385	615.41	1375	114.58	829	69.08	July, Aug., Oct.	Dec., Jan.	0.186
4.5	708	....	......	....	......	627	52.25	....	....	....

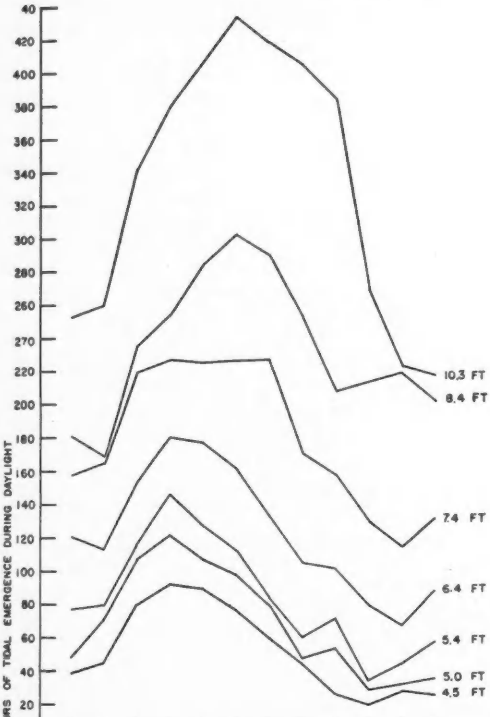

FIG. 5. Total tidal emergence during daylight hours for each month of the year. Note shift in the peak from June at levels higher than 7.4 ft. to April at levels lower than 7.4 ft. Elevations are in feet above M.L.L.W.

THE SPARTINETUM

It was suggested by Johnson & York that wherever the vertical distribution of the *Spartinetum* could be measured, it would be found to lie midway between the mean tide levels. On the Palo Alto marshes this does not seem to be true. On these marshes, it will be recalled, mean higher high water is 8.4 ft. above mean lower low water, while the half tide level is 4.5 ft. above mean lower low water. The *Spartinetum* ranges vertically between 5.4 and 8.4 ft. above mean lower low water, thus forming a belt along the level of mean high water (7.8 ft. above mean lower low water). It extends vertically above mean high water to the level of mean higher high water, which forms its upper limit. It was not found to extend below 5.4 ft. in the area studied, yet if Johnson and York's prediction held true for this marsh, it could be expected that the *Spartinetum* would occur around 4.2 ft. above M.L.L.W., or approximately at half tide level.

Spartina leiantha is the dominant seed plant below the 6.4-foot level of the marsh. It has a vertical range of 3 ft.—a range which overlaps that of the glasswort by 2 ft. At its upper level, 8.4 ft. above M.L.L.W., the *Spartinetum* is subject to an average of 9.7 days per month of tidal emergence during daylight. The maximum emergence in daylight at 8.4 ft. above M.L.L.W. is 302 hours (equivalent to 12.5 days) occurring in June, while the minimum exposure in daylight is 169 hours (7.04 days), occurring in February (Fig. 5). There is a total yearly emergence of 4857 hours (an average of 16.8 days per month), while the total submergence for the year is 3901 hours (an average of 13.4 days per month). The emergence-submergence ratio is 1.25 (Table I).

The maximum number of hours of daylight emergence at 5.4 ft. above M.L.L.W.—the lowest recorded extent of cord-grass—is 146 hours (6.08 days), occurring in April, while the minimum period of daylight emergence is 34 hours (1.41 days), occurring in October. It has an average emergence from the tide during the daylight hours of 3.45 days per month. The total yearly emergence at this level is 1721 hours, an average of 5.93 days per month, with a total of 7039 hours of submergence, an average of 24.3 days per month. The emergence-submergence ratio is 0.24.

The months of maximum daylight submergence for the upper limits of the cord-grass then are the autumn months when the grass is at the end of its flowering and beginning to turn brown, the new year's growth not yet having appeared through the muck. During these months, growth on the marsh is slowing to a minimum (Purer 1942) and the rains begin and increase steadily. At the lower limit of the *Spartinetum*, 5.4 ft. above M.L.L.W., the maximum daylight submergence also occurs late in the year—October, November, and December—months when there are respectively 14, 12, and 11 days with no tidal emergence whatever during the daylight hours. Since the new shoots begin to appear in December and the old stalks and leaves are drying up, submergence during the whole period of daylight could be expected to reduce photosynthesis markedly. There may be only one, two, or three hours during which photosynthesis might occur freely on days when emergence occurs during daylight.

Aeration would also be at a minimum during such long periods of inundation, for the short new shoots of the cord-grass are often completely submerged during the hours when gaseous exchange through the stomata would ordinarily be at a maximum. It is significant that the only phanerogam to grow luxuriantly on the Palo Alto marsh under such rigorous conditions is one with an extensive aerenchyma.

It will be recalled that Johnson & York found that the cord-grass at its lower margin endured a submergence of about 8.5 hours at each tide, or 17 hours of daily submergence. At its upper margin, Spartina was subjected to a soil submergence of only 2.5-3 hours per day. Arber (1934) stated that *Spartina townsendi* on the southern coast of England and the northern coast of France could bear about 6 consecutive hours of submergence.

On the Palo Alto marshes, the cord-grass growing at 8.4 ft. above M.L.L.W. endures a maximum submergence of 8 consecutive hours during the higher high water in February, and a maximum of 6 consecutive hours of submergence during the low high water, or 14 hours of submergence on a day of maximum submergence. At the lower margin of the *Spartinetum* (5.4 ft. above M.L.L.W.) the maximum daily submergence reaches as much as 21 consecutive hours when the low water between two high waters is not low enough to expose the 5.4-foot elevation. This seems to be the maximum submergence that can be endured by the cord-grass, for at 5.0 ft. above M.L.L.W., the maximum number of consecutive hours of submergence is 22, and no plants of the cord-grass were recorded at that elevation. At 5.4 ft. M.L.L.W., there are 6 more hours of exposure during October (the month of maximum submergence) than there are at the 5.0-foot level. The increased submergence, with the subsequent decrease in exposure at an elevation just 0.4 ft. lower is probably decisive in preventing the invasion of the cord-grass. Spartina is able to endure a tremendous amount of submergence on the Palo Alto marsh compared to that it endured at Cold Spring Harbor, but the submergence borne by *Spartina alterniflora* on the Romney marsh (Chapman 1940) approximates that to which *S. leiantha* is subject on the Palo Alto marshes. At Romney, *S. alterniflora* extends down to 2.81 ft. above mean low water and endures an average submergence per day of 16.25 hours. The average exposure per day at Romney is 7.75 hours, July is the month of maximum submergence, and January is the month of maximum emergence.

The upper range of the *Spartinetum* overlaps the lower range of the *Salicornietum* by 2 ft., so that Spartina and Salicornia are frequently intermingled on the marsh. The Salicornia under such circumstances is usually not vigorously developed, but in some instances isolated individuals of the cord-grass may be found several feet beyond the margin of the *Spartinetum*, surrounded by a vigorously developed *Salicornietum* (Fig. 6B). If, as the accepted idea has been, the Spartina has an upper limit to its range because of its inability to compete with the glasswort, it becomes difficult to explain an apparent advance of the *Spartinetum* into the *Salicornietum*. It would be expected that conditions on the marsh are changing to favor the advance of the *Spartinetum*, i.e. the land is sinking, resulting in an increased inundation time at higher levels, thus forcing the retreat of the glasswort with a subsequent advance by the *Spartinetum*. It would seem more likely, however, that the isolated individuals of Spartina in the *Salicornietum* are relics of the *Spartinetum* which is now retreating as the elevation of the marshland is slowly raised by silting, thus favoring the advance of the glasswort. Purer (1942) noted that the glasswort invades the cord-grass only after sufficient debris has accumulated to raise the level of the ground. Such changes occur slowly on the marsh, however, so that a number of years of observation would be required to determine the nature of the events taking place.

THE SALICORNIETUM

Salicornia ambigua is the dominant seed plant above the 8.4-foot level on the marsh. It has a vertical range of four feet, the lower two feet coinciding with the upper range of *Spartina leiantha*. At its upper level, 10.3 ft. above M.L.L.W., it is subjected to an average of 13.8 days of exposure per month. The maximum emergence during daylight of 433 hours (18.04 days) occurs in June, while the minimum emergence in daylight is 222 hours (9.25 days) in November (Fig. 5). There is a total yearly emergence at 10.3 ft. M.L.L.W. of 7107 hours (an average of 24.66 days per month) and a total annual submergence of 1753 hours, averaging 6.08 days per month. The emergence-submergence ratio is 4.05 (Table I).

At its lowest recorded level, 6.4 ft. above M.L.L.W., the Salicornia is subjected to an average of 5.12 days of tidal emergence per month during daylight. The maximum daylight emergence at this level is 180 hours or an equivalent of 7.5 days, occurring in April,

FIG. 6A. Silt-laden tide water inundates Spartina at every tide on the mud flats, thus reducing hours per day of effective photosynthesis.

FIG. 6B. The *Salicornietum* with relics of the *Spartinetum* in middleground. Compare heights of Spartina and Salicornia.

while the minimum exposure is 67 hours—2.79 days—in November. The total yearly emergence at 6.4 ft. above M.L.L.W. is 2734 hours, an average of 9.48 days per month, while the total submergence is 6026 hours, or an average of 20.9 days per month. The emergence-submergence ratio is 0.45.

The glasswort is widely distributed on the Palo Alto marshes. There are broad stretches of *Salicornietum* which are either pure stands of Salicornia or which have Frankenia or Distichlis intermingled in lesser or greater abundance. Even local elevations low on the marsh are covered with Salicornia, sometimes with cord-grass intermingled. This, too suggests the gradual elevation by silting of low areas in the *Spartinetum* as has been suggested in the previous section.

It has been pointed out that the glasswort grows luxuriantly in areas where the drainage and aeration are comparatively good. This is particularly true along the margins of the drains where undercutting by the tidal current insures good drainage and, augmented by crab burrows in the banks, good aeration. Salicornia has no aerenchyma, and for this reason has been thought incapable of enduring the degree of inundation to which Spartina is accumstomed. Even though the lower margin of the *Salicornietum* is only one foot above the lowest occurence of the *Spartinetum*, the Salicornia is subjected to 34 additional hours of daylight exposure during April, the month of maximum tidal emergence, and 23 additional hours of exposure in daylight in November, the month for the maximum exposure for the *Salicornietum* below 6.4 ft. above M.L.L.W. (Fig. 5). As can be seen from Table I, the lowest extent of the *Salicornietum* is subject to an average of 502.1 hours of submergence per calendar month (an equivalent of 20.9 days of submergence per month) as compared with the average of 586.5 hours of submergence per month (an equivalent of 24.4 days of submergence per month) at 5.4 ft. above M.L.L.W. At its lowest extent, Salicornia is frequently poorly developed, being shorter than usual and sparsely distributed.

Salicornia spreads by seeding and in the early spring—February and March—seedlings are abundant particularly upon areas which have been cleared of vegetation.

At its upper limit on the Palo Alto marsh, the *Salicornietum* does not merge into any particular formation. In several places it ends abruptly where fills have been made, while in still other sections it extends up to the road where it either ends abruptly or mingles briefly with *Chenopodium ambrosioides*, *Cotula coronopifolia*, and other plants which have followed the road into the marsh.

THE DISTICHLIDETUM

The highest recorded occurrence of *Distichlis spicata* on the marshes near the Palo Alto Yacht Harbor was at 10.2 ft. above M.L.L.W. At this level it is subject to approximately the same conditions of emergence and submergence as is Salicornia. Its lowest extent onto the marsh however was recorded at 7.15 ft. above M.L.L.W. At its lower level, the salt-grass is exposed to a maximum daylight emergence of 226 hours (equivalent to 9.4 days) during the months of June and July, and a minimum daylight exposure of 114 hours (or 4.7 days) in November (Fig. 5). There is a total yearly emergence of 3501 hours, equivalent to an average of 12.15 days

per month, while there is a total of 5259 hours of submergence per year, or an equivalent of 18.26 days per month. The emergence-submergence ratio is 0.67 (Table I).

Salt-grass is widely distributed on the marsh but is to be found only occasionally in pure stands. When these stands occur, they usually are to be found on the tops of the levees. Generally, Distichlis intermingles with Salicornia, Frankenia, or Jaumea, but is found only occasionally intermixed with Spartina.

JAUMEA CARNOSA AND FRANKENIA GRANDIFOLIA

Jaumea carnosa has a vertical range of 1.35 ft. and throughout its range is subjected to the same conditions of submergence and inundation as Salicornia and as is Spartina at the upper levels of its range. It is widely distributed in some sections of the marsh, generally intermingled with *Frankenia grandifolia* or *Distichlis spicata.* It is not infrequently found intermingling with the cord-grass, particularly at the edge of the *Spartinetum.* Occasionally it is found in pure stands along the levees, but these stands are never very extensive.

Frankenia grandifolia has a vertical range of 2.8 ft., its upper range being equivalent to that of Salicornia, while its lower range extends slightly below that of *Jaumea carnosa.* It is found occasionally in pure stands along the levee, where it may assume a woody, gnarled, shrubby structure when subjected to wave action at every tide. Generally Frankenia is found intermingled with the various other plants of the marsh.

Apparently neither of these plants can descend to lower levels on the marsh because of the submergence time to which they would be exposed.

SUMMARY AND CONCLUSIONS

The marshes around the Palo Alto Yacht Harbor on San Francisco Bay support three major vegetational associations; a) the *Salicornietum,* with the glasswort *Salicornia ambigua* as the dominant; b) the *Spartinetum,* in which the cord-grass *Spartina leiantha* is the dominant; and c) the *Distichlidetum* with *Distichlis spicata,* the salt-grass, as the dominant. The Spartina extends from 8.4 ft. above M.L.L.W. down to 5.4 ft. above M.L.L.W.; the glasswort occurs from 10.3 ft. above M.L.L.W. to 6.4 ft. above M.L.L.W.; and the salt-grass is found between 10.3 ft. and 7.15 ft. above M.L.L.W.

The vertical distribution of these seed plants is effectively controlled by the degree of tidal emergence and submergence to which they are subjected. The cord-grass at times endures a maximum submergence of 21 continuous hours at its lowest occurrence. Even a slight increase in submergence time seems to be unendurable, preventing the colonization of the tidal mud flats below the 5.4 ft. level above M.L.L.W. This same factor prevents the Salicornia, which lacks air-storage space, from extending its range lower than 6.4 ft. above M.L.L.W. At its upper extent, the glasswort abruptly disappears where man-made improvements on the marsh have raised the elevation to the point where plants of higher elevations may invade. At no point was it found to give way to a *Scirpetum* or *Juncetum* as so often happens on the salt marshes of the Eastern coast of the United States.

The upper 2 ft. of the range of the *Spartinetum* coincide with the lower 2 ft. of the range of the *Salicornietum.* It is believed that this coincidence is a result of a gradual increase in elevation due to reclamation activities on the marsh, and that the *Salicornietum* will eventually replace the *Spartinetum,* which will become increasingly restricted in occurrence as reclamation continues.

Distichlis spicata is widely distributed on the marsh, but is to be found only occasionally in pure stands, usually on the tops of the dikes. Generally, Distichlis intermingles with the glasswort, but it is only occasionally found occurring with Spartina. The salt-grass, however, is not so well-adapted to living under conditions of prolonged submergence as is Spartina with its extensive aerenchyma.

Jaumea carnosa and *Frankenia grandifolia* are frequently found occurring with the salt-grass, but neither inhabits the lower levels of the marsh.

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